

Tamm Review: Deep fine roots in forest ecosystems: Why dig deeper?

Amandine Germon^{a,b}, Jean-Paul Laclau^{a,b,c}, Agnès Robin^{b,c,d}, Christophe Jourdan^{b,c,*}

^a UNESP, São Paulo State University, School of Agricultural Sciences, Botucatu, São Paulo 18610-307, Brazil

^b Eco&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France

^c CIRAD, UMR Eco&Sols, F-34060 Montpellier, France

^d ESALQ, Soil Science Department, Escola Superior de Agricultura, Luiz de Queiroz, Universidade de São Paulo, CEP 13418-900 Piracicaba, SP, Brazil



ARTICLE INFO

Keywords:

Deep rooting
Root growth
Root traits
Carbon sequestration
Water uptake
Nutrient uptake
Deep mycorrhizas

ABSTRACT

While the number of studies dealing with fine root dynamics in deep soils layers (depth > 1 m) has increased sharply recently, the phenology, the morphology, the anatomy and the role of deep fine roots are still poorly known in forest ecosystems. This review summarizes the current knowledge on fine root production, mortality and longevity in deep soil layers, mycorrhizal association with deep roots, and the role of deep fine roots on carbon, water and nutrient cycling in forest ecosystems. Plant species are known to be more deeply rooted in tropical ecosystems than in temperate and boreal ecosystems, but deep-rooted species are common in a wide range of climates. Deep fine roots are highly plastic in response to changes in environmental conditions and soil resources. Recent studies show that functional traits can be different for deep and shallow roots, with a possible functional specialization of deep fine roots to take up nutrients. With higher vessel diameter and larger tracheid, the anatomy of deep fine roots is also oriented toward water acquisition and transport by increasing the hydraulic conductivity. Deep fine roots can have a great impact on the biogeochemical cycles in many forests (in particular in tropical areas where highly weathered soils are commonly very deep), making it possible to take up water and nutrients over dry periods and contributing to store carbon in the soil. The biogeochemical models in forest ecosystems need to consider the specificity of deep root functioning to better predict carbon, water and nutrient cycling as well as net ecosystem productivity.

1. Introduction

Roots have an essential role in forest ecosystems through the mechanical function of tree anchorage and the physiological function of absorbing and transporting the amounts of water and nutrients needed for plant development (Pregitzer et al., 2002; McCormack and Guo, 2014). The anchorage function is mainly enabled by physical interactions between the roots and the soil. The absorptive function is more complex as it involves biogeochemical interactions between fine roots, soil particles and soil biota, with sometimes symbioses between fine roots and soil bacteria or fungi. Fine roots, commonly considered as root with a diameter lower than 2 mm (McCormack et al., 2015), have the ability to adapt to changing environments to facilitate plant development. Fine root activity can modify physical, chemical and biological soil properties, which can have repercussions at the plant level but also at the ecosystem level (McCormack et al., 2015). Indeed, fine roots play a major role in carbon (C) cycling in forest ecosystems, with large C inputs into the soil through root exudates and necromass production, as well as large C returns to the atmosphere through root

respiration and decomposition processes (Balesdent and Balabane, 1996; Strand et al., 2008). The great plasticity of root systems, both architecturally and functionally, can be strongly influenced by plant phenology, soil properties and climatic conditions (Hodge et al., 2009). Fine root dynamics have been studied quantifying production and mortality (Hendrick and Pregitzer, 1993; McCormack and Guo, 2014), turnover and survivorship (Anderson et al., 2003), senescence (Huck et al., 1987) and elongation rates (Germon et al., 2016; Lambais et al., 2017). Fine root dynamics are driven by exogenous factors like soil temperature and water content (Coll et al., 2012) and endogenous factors like hormone productions (McAdam et al., 2016) and photosynthate and nutrient allocations within the plant (Tierney and Fahey, 2002; Sloan et al., 2016).

Binkley (2015) pointed out the critical need to include depth and timescale of ecological processes below the soil surface in a modern conceptualization of forest ecosystems. The full 'critical zone' concept from Earth science should be included in conventional thinking about ecosystems and deep roots can be a key functional element of the Critical Zone (Richter and Billings, 2015; Pierret et al., 2016). Shrub and

* Corresponding author at: CIRAD, UMR Eco&Sols, F-34060 Montpellier, France.

E-mail address: christophe.jourdan@cirad.fr (C. Jourdan).

tree roots have the ability to explore huge volumes of soil and can be found at great depths in xeric environments (Canadell et al., 1996; Schenk and Jackson, 2002). Deep roots improve tree tolerance to drought (McDowell et al., 2008; Nardini et al., 2016) and store C in deep soil layers (Balesdent et al., 2018). Understanding the spatial and temporal variability of fine root functioning in deep soil layers is needed to improve our understanding of biosphere-atmosphere interactions (Zeng et al., 1998; Kleidon and Heimann, 2000), and the accuracy of terrestrial biosphere models (Saleska et al., 2007; Christoffersen et al., 2014). Even though the importance of deep root systems has been highlighted in several reviews focused on trees (Canadell et al., 1996; Maeght et al., 2013; Pierret et al., 2016) or on crops (Thorup-Kristensen et al., 2020), the functional significance of deep fine root dynamics, and their contribution to biogeochemical cycles are still poorly documented. Maeght et al. (2013) proposed to consider as deep roots the roots growing at a depth of >1 m. Even though fine root densities are low at great depths, deep roots are likely to play a key role in many processes of plant physiology, community ecology and biogeochemistry in forest ecosystems. Deep roots are found in many biomes where drought periods can occur (Nepstad et al., 1994; Canadell et al., 1996; Jackson et al., 2000; Schenk and Jackson, 2002). However, the maximum rooting depth reported in the scientific literature is commonly underestimated because most studies did not sample soils down to the root front, which artificially truncated root distributions (Freycon et al., 2015). In a review paper, Stone and Kalisz (1991) reported 37 examples of root systems observed between 10 and 60 m below the soil surface, indicating that the maximum rooting depth can vary considerably with climatic and soil conditions as well as between tree species. In another review paper, Canadell et al. (1996) estimated that roots extend in deep horizons down to 9.5 ± 2.4 m in deserts, 7.3 ± 2.8 m in tropical evergreen forest and 15.0 ± 5.4 m in tropical grassland and savannah, with a maximum rooting depth of 68 m reported for *Boscia albitrunca* trees in Botswana. Schenk and Jackson (2002) showed in a meta-analysis that the maximum rooting depth increased for plants growth forms as their size and life span increased, with the highest values for trees and shrubs (Fig. 1).

Distributions and dynamics of deep roots are still poorly documented relative to shallow roots (Richter and Billings, 2015; Pierret et al., 2016). Despite recent technical innovations, the observation of deep roots remains difficult, time-consuming, expensive and requires a

combination of methods to obtain reliable results (Maeght et al., 2013). Direct and indirect techniques can be used for monitoring deep roots depending on the research aim (Vogt et al., 1998; Hendricks et al., 2006). Deep root functioning at considerable soil depths has been indirectly studied by quantifying water, nitrogen and carbon budgets of the ecosystem (Vogt et al., 1998). Direct methods based on soil excavation, trenches, sequential coring, ingrowth cores, and rhizotron observations have been used to monitor root dynamics *in situ* (Maeght et al., 2013). Both indirect and direct approaches can have potential biases leading to overestimate or underestimate root growth and root decomposition. There is no consensus on the most effective and reliable method that should be used to quantify fine root dynamics.

Several attempts in plant root architecture and development modelling were performed so far without considering deep rooting patterns. Some models were based on a continuous formalism through partial derivative equations that simulate root apex density and root interaction through time and space (Bastian et al., 2008; Dupuy et al., 2010; Bonneau et al., 2012). These types of models enabled direct coupling with water transport models (Doussan et al., 1998), or nutrient uptake competition models (Bonneau et al., 2012; Mayer et al., 2012; Gérard et al., 2017). Other models were based on a discrete and/or random formalism that simulates root architecture, growth, branching and death processes. Some of them were based on mathematical processes such as L-systems (Leitner et al., 2010) or fractals (van Noordwijk et al., 1994; Ozier-Lafontaine et al., 1999), or using combinations of the two (Shibusawa, 1994), others were derived from direct measurements performed on real plants taking into account root-soil interaction functions (Diggle, 1988; Jourdan and Rey, 1997a,b; Lynch et al., 1997; Pagès et al., 2004; Dunbabin et al., 2013; Pagès et al., 2014; Barczy et al., 2018), with water and nutrient uptake (Wu et al., 2007; Javaux et al., 2008; Leitner et al., 2010; Postma et al., 2017). Most of these models, with the exception of some of them (Jourdan and Rey, 1997a, b; Pagès et al., 2014; Barczy et al., 2018), are mainly designed for annual and herbaceous plants, with a short lifespan and a limited rooting depth. For perennial crops, shrubs and trees with longer lifespans and deeper rooting strategies, previous models do not consider possible changes in root architecture, diameter, growth, mortality, or functioning processes depending on (great) soil depth. A first attempt was made with the DigR model, which manages parameter values that may change depending on the position along roots of each type, changing with soil depth or not (Barczy et al., 2018).

Our paper provides an up-to-date literature review on morphological and phenological traits of fine roots along deep soil profiles in forest ecosystems. The production, mortality rates and longevity of deep fine roots, as well as symbiosis with mycorrhizas, their role in water and nutrient uptake and their influence on belowground C sequestration are reviewed. We addressed the following questions: (1) How can environmental conditions, soil resources and symbiotic association along deep soil profiles influence the functioning of fine roots and their main functional traits? (2) Do we need to take into consideration the specificity of deep fine roots to improve current predictions of C, water and nutrient cycling in forest ecosystems? We proposed a conceptual scheme summarizing how root traits vary between the topsoil and deep soil layers (Fig. 2).

2. Morphology and anatomy of deep fine roots

The morphology and architecture of root systems vary greatly between plant species but also within individual species (Cannon, 1949; Nibau et al., 2008). Biogeochemical processes in forest ecosystems are strongly influenced by root architecture (Addo-Danso et al., 2020), as well as the ability of plants to survive under stressful conditions (Penuelas et al., 2013). Functional traits of fine roots vary with environmental conditions and resource distribution (Ostonen et al., 2007). Fine roots have been classified depending on their main functions and metabolic activity either in absorptive roots involved in the

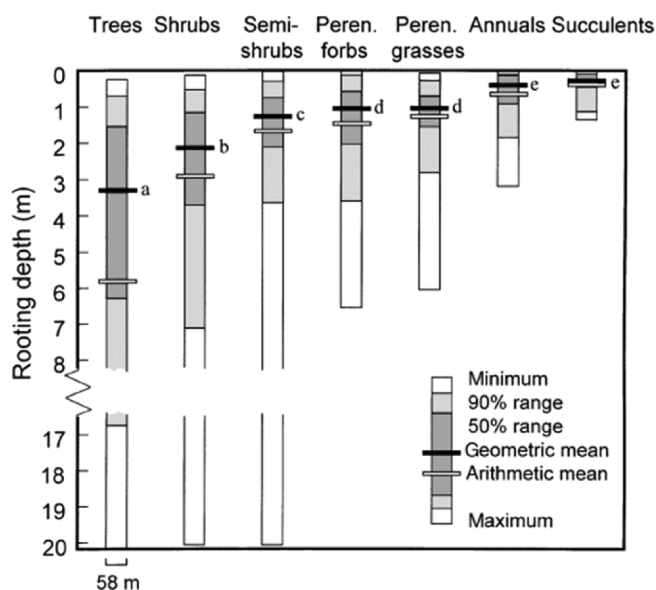


Fig. 1. Maximum rooting depths of plant growth forms. Geometric means marked by different letters were significantly different according to one-way ANOVAs. Source: Schenk and Jackson (2002), used by permission.

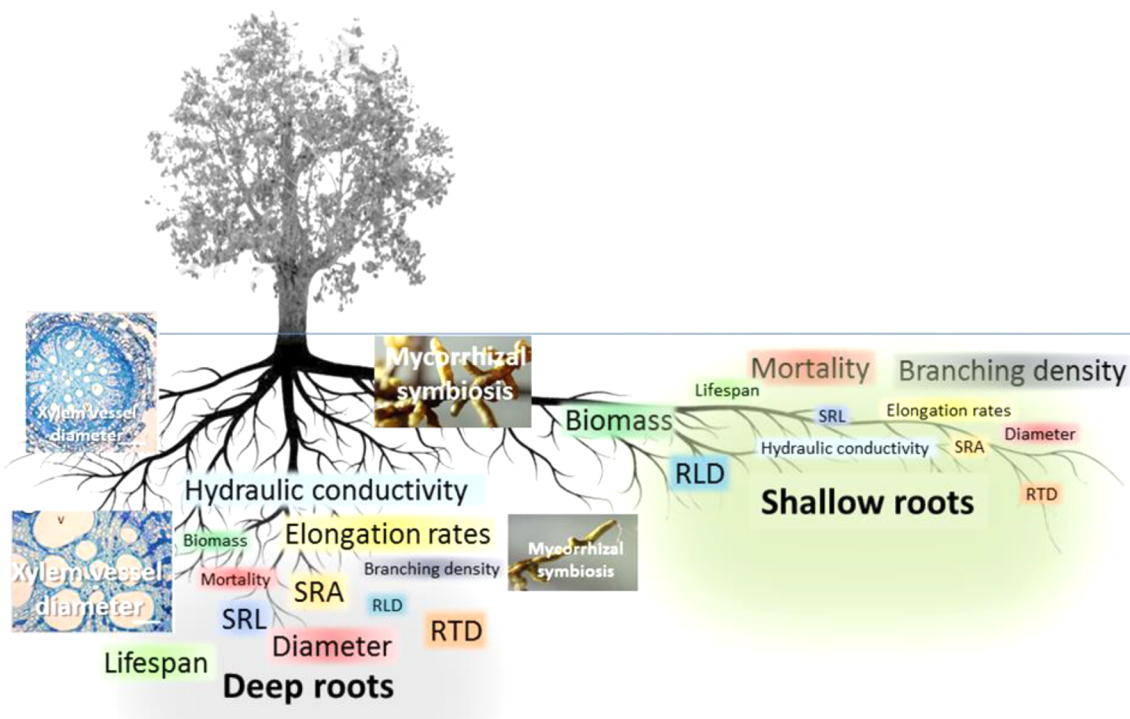


Fig. 2. Conceptual scheme of root trait variations between the topsoil and deep soil layers. The larger the size of the text, the higher the value of the root trait considered. The main tendencies in the literature (indicated in [Appendix A](#)) are shown here, but the behavior of certain plant species can be different. RLD for root length density, SRL for specific root length, SRA for specific root density and RTD for root tissue density. Images of root anatomy and ectomycorrhizal symbiosis were adapted from Perron-Gomide *et al.* (Com. Pers. 2020) and Robin *et al.* (2019), respectively.

capture and uptake of soil resources that are extremely fine and are the most distal roots, or in roots involved in the transport of water and nutrients that are larger roots, higher in the branching order, and constitute most of the structural part of the root system (McCormack *et al.*, 2015). The high variability of environmental conditions such as soil moisture and temperature or resource (water and nutrients) availability along soil profiles result in contrasting fine root functional traits with soil depth.

Fine roots have been commonly considered as a coherent “pool” of an arbitrary 0–2 mm root diameter class with the same dynamics, turnover rates, respiration costs and the same rates of water and nutrient uptake (Persson, 1980; Jackson *et al.*, 1997). However, an increasing number of recent studies suggest that fine root functions can vary depending on the root order of the branching root system (Pregitzer *et al.*, 1997; Majdi *et al.*, 2001; Pregitzer *et al.*, 2002; Guo *et al.*, 2004; Wang *et al.*, 2006; Hishi, 2007; Wang *et al.*, 2007; Pregitzer, 2008; Valenzuela Estrada *et al.*, 2008; Comas and Eissenstat, 2009; Fan and Guo, 2010; Rewald *et al.*, 2011; Beyer *et al.*, 2013; Rewald *et al.*, 2018; Wada *et al.*, 2019). These studies have clearly shown that several fine root traits such as diameter (D), length (L), specific root length (SRL), specific root area (SRA), root length density (RLD), branching density but also number of xylem vessels, tissue density, C/N ratios, phenolic, lignin and suberin contents, mycorrhizal colonization and median lifespans varied depending on the root order. The highest fine root order number, the coarsest root diameter, the highest median lifespan, tissue density, xylem vessel number, lignin and suberin content, and the lowest length, branching density, RLD, SRL, SRA, C/N ratios, and mycorrhizal colonization.

Fine root exploration in deep soil layers represents a high metabolic cost for plants (Iversen, 2010), which may influence fine root traits (Prieto *et al.*, 2015). Specific root length (SRL) and specific root area (SRA) can be affected by soil depth (Maurice *et al.*, 2010; Prieto *et al.*, 2015; Pinheiro *et al.*, 2016), while other functional traits (concentrations of C, N, cellulose, lignin,...) seem less sensitive (Prieto *et al.*,

2015). SRL and SRA values are positively correlated with the soil volume in contact with fine roots, which influences the plant capacity to take up limited soil resources (Addo-Danso *et al.*, 2020). Changes in specific root length and specific root area with soil depth have been little investigated and the trends are not clear (Makita *et al.*, 2011; Prieto *et al.*, 2015; Pinheiro *et al.*, 2016). Pinheiro *et al.* (2016) showed a slight increase in SRL and SRA with soil depth down to 13.5 m for 4 genotypes of several *Eucalyptus* species in Brazil. Maurice *et al.* (2010) also found that SRL increased with soil depth (down to 3 m) in *Eucalyptus* plantations of different ages. On the contrary, SRL decreased with soil depth down to 1.2 m in *Pinus pinaster* plantations in France (Bakker *et al.*, 2009). Adriano *et al.* (2017) found no significant changes in SRL with soil depth down to 8 m in *Citrus sinensis* plantations, but they observed a tendency toward an increase in mean fine root diameters. Gwenzi *et al.* (2011) also found that fine root thickness tended to increase with soil depth (down to 1.4 m) in *Acacia rostellifera* and *Melaleuca nesophila* plantations in Western Australia. Prieto *et al.* (2015) measured fine root functional traits in 20 plant communities under tropical climate, montane climate, and sub-humid Mediterranean climate. They showed that fine roots were thicker in deep soil layers (down to 1.6 m) compared to the topsoil. On the contrary, Sochacki *et al.* (2017) observed that root diameter decreased with depth down to 6 m in *Eucalyptus globulus* plantations in southwest Australia. Mixing tree species can also greatly influence SRL and SLA but studies comparing fine root traits in mixture with the monospecific stands along deep soil profiles are scarce. Germon *et al.* (2018) showed that SRL and SRA values in mixed-species stands of *Acacia mangium* and *Eucalyptus grandis* were 110–150% and 34% higher, respectively, than in their monoculture, and the same pattern was observed between the topsoil and a depth of 6 m. Fast-growing species require a rapid and efficient acquisition of resources above and belowground, which generally translate into higher SRA and SRL values compared to slow-growing species, in particular in deep soil layers (Ryser, 2006; Reich, 2014; Jo *et al.*, 2015). High SRL and thin roots are often associated with a better

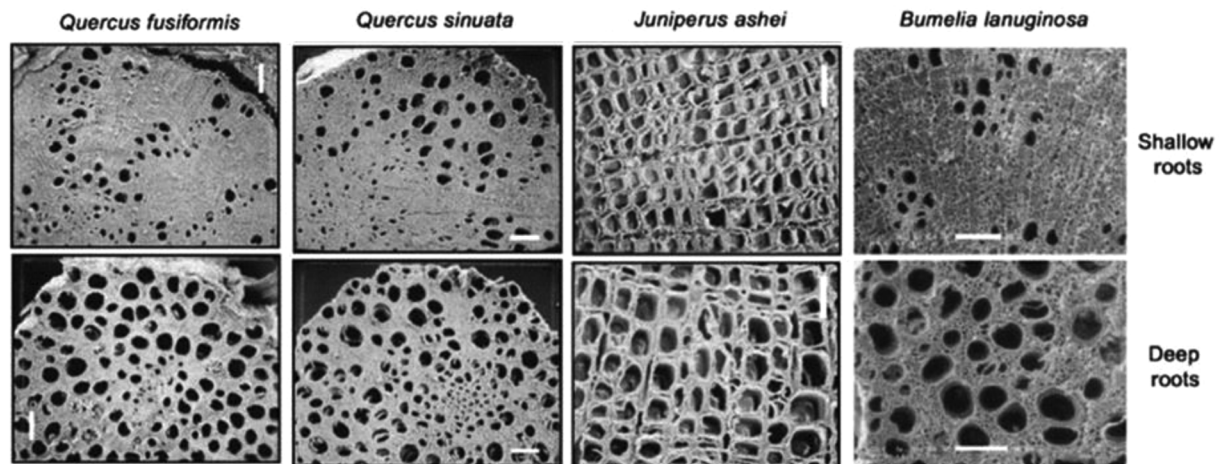


Fig. 3. Scanning electron micrographs of shallow roots (top row) and deep roots (bottom row, depth of 18–20 m) for *Quercus fusiformis*, *Juniperus ashei*, *Quercus sinuata* and *Bumelia lanuginosa* tree species from the Edward's Plateau region of central Texas. The white line in each sub-figure shows the scale for a length of 50 μm for *Juniperus ashei*, 300 μm for *Quercus sinuata* and *Quercus fusiformis*, and 200 μm for *Bumelia lanuginosa*. Adapted from McElrone et al. (2004), used by permission.

capacity to capture soil resources (Hodge, 2004). Establishing a deep root system with a high area of contact between soil and fine roots (through high fine root density and SRA values) makes it possible to withdraw water from a large soil volume (Jackson et al., 2000).

Deep roots are mainly oriented toward water acquisition and transport. McElrone et al. (2004) showed that deep roots of *Juniperus ashei*, *Bumelia lanuginosa*, *Quercus fusiformis* and *Quercus sinuata* had higher vessel diameter and larger tracheid than shallow roots in deep soil layers, down to a depth of 18–20 m, with higher hydraulic conductivity (Fig. 3). Similar results were found for eucalypt fine roots in Brazil, where xylem vessels were less abundant but with a larger diameter at depth > 10 m than shallow roots of the same diameter class (Perron-Gomide et al., Com. Pers. 2020). In line with those results, Pate et al. (1995) showed that roots at a depth of 2 m had larger xylem conduits, higher SRL and SRA values, as well as hydraulic conductivities up to 15 times higher than roots in shallow layers for tree and shrub species of *Proteaceae* (*Banksia prionotes*, *Banksia ilicifolia* and *Adenanthos cygnorum*) in Australia. Physiological and anatomical adjustments of fine roots in deep soil layers might be an adaptation of plants to maximize their hydraulic efficiency (McElrone et al., 2007). Even those promising results suggesting that very deep roots, despite their scarcity, could have a key role to take up water during drought periods, studies dealing with fine root morphology and anatomy at great depth are still scarce.

3. Phenology of deep fine roots

Fine roots in deep and shallow soil layers exhibit contrasting phenology with an asynchrony of growth. Maeght et al. (2015) showed that shallow fine root growth of *Hevea brasiliensis* was synchronized with rainfall events and ceased during the dry season. On the contrary, fine root growth occurred at the end of the wet season and continued over the dry season at a depth of > 2.5 m. Germon et al. (2016) also observed an asynchrony between the growth of shallow and deep roots in an agroforestry system with walnut and durum wheat in the south of France. While the growth of tree roots in the topsoil occurred mainly in summer, root growth during the rainy period (in winter) was mainly observed at a depth of > 2.5 m. The same behavior has been shown in tropical *Eucalyptus* plantations growing in very deep soils in Brazil. An asynchrony between shallow and deep root growth was observed, with fine root growth occurring in the topsoil over the rainy summer while it peaked deeper than 3 m at the end of the dry season (Lambais et al., 2017). In another *Eucalyptus grandis* stand, Germon et al. (2019) showed a negative correlation between the amount of extractable water

in the topsoil and the flushes of fine root growth in very deep soil layers. In those plantations, fine root growth in deep soil layers seems to be related to the overall water demand of the whole tree and controlled by the need to use increasingly deeper water resources when water becomes scarce in the topsoil, which is consistent with modeling studies (Christina et al., 2017, 2018). Vertical growth rates of trees were almost symmetrical above- and below-ground in *Eucalyptus* plantations, reaching 10.4 and 19.2 m in height and a maximum rooting depth of 9.2 and 15.8 m at 1.5 and 3.5 years after planting, respectively (Christina et al., 2011). Other studies using different methodologies (deep drilling, observations on trench walls, injection of ^{15}N tracer) in the same area confirmed this velocity of root front displacement (Lacrau et al., 2013b; Pinheiro et al., 2016, 2019). The growth rates of *Eucalyptus* roots observed on minirhizotrons by Lambais et al. (2017) are consistent with this downward speed of exploration, with mean elongation rates increasing with soil depth up to a maximum value of 3.6 cm day^{-1} over a short period below 3 m. In another *Eucalyptus grandis* stand, minirhizotron observations confirmed higher fine root elongation rates in deep soil layers than in the topsoil (Fig. 4), reaching a maximum of 4.3 cm per day over a short period at depths below 5 m (Lacrau et al., 2013b; Germon et al., 2016; Lambais et al., 2017; Germon et al., 2019).

Increasing root growth rates with soil depth could be an adaptation to drought (Annerose and Cornaire, 1994), providing a rapid access to large amounts of water stored in deep soil layers (Christina et al., 2017). This pattern suggests a positive feedback from root growth downward to shoot growth (Friend et al., 1994). Environmental conditions and plant growth regulators may control root exploration of deep soil layers (López-Bucio et al., 2003). Soil water contents are commonly higher in deep soil layers and variations of temperature are lower than in the topsoil (Du and Fang, 2014; Radville et al., 2016). Climatic factors are buffered in deep soil layers, fluctuating less throughout the day and the seasons than in the upper layers, which influences differentially root phenology along deep soil profiles. Changes in fine root phenology with soil depth might also be controlled by other factors. As deep roots are more distant from the shoot than shallow roots, photosynthates might take more time to reach deep roots.

The longevity of fine roots generally increases with soil depth (Hendrick and Pregitzer, 1996; Baddeley and Watson, 2005) but root behavior at depth may be different in some situations. Wells et al. (2002) showed that root longevity of *Prunus persica* significantly increased with soil depth down to 1.6 m. Germon et al. (2016) showed that the mortality of walnut roots was higher in the topsoil than in deep

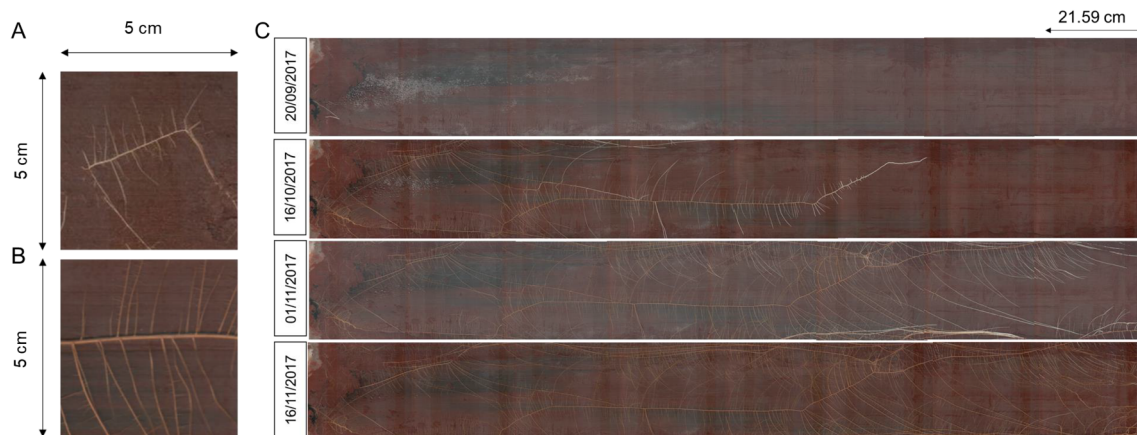


Fig. 4. Images of *Eucalyptus* fine roots in the topsoil (A), and at depth of 11.5 m (B) in minirhizotron tubes installed in deep permanent pits in Brazil showing great differences in branching density of very fine roots. The velocity of exploration of deep soil layer in this stand (C) is shown scanning the same 1.8-m long minirhizotron tube inserted at a depth of 11.5 m from September 20, 2017 to November 16, 2017. Adapted from Germon (2019).

soil layers with a median life span of 167 days within the first soil meter and 208 days in the 2.5–4.7 m layer in an agroforestry system in the south of France. On the contrary, Maeght et al. (2015) found that root lifespan decreased with soil depth in a rubber tree plantation in Thailand, from 180 to 250 days between the depth of 1 and 2.5 m to 120 days between 3 and 4.5 m. Lambais et al. (2017) found no significant differences in the lifespan of *Eucalyptus* fine roots between the topsoil and a depth of 6 m in Brazil. The relationship between depth and fine root longevity is therefore probably dependent on the eco-physiology of tree species as well as on local environmental parameters (e.g., temperature, water content, N availability, CO₂ and probably O₂ partial pressure) (Vogt et al., 1995). There are still major uncertainties about the mechanisms controlling fine root phenology in deep soil layers (Radville et al., 2016).

4. Fine root biomass and carbon sequestration in deep soil layers

Soil C storage may be strongly underestimated because most studies have focused on the topsoil (Harrison et al., 2011; Callesen et al., 2016). While fine roots play a major role in the global carbon cycle, their contribution on soil C storage in very deep soil layers remains little understood (Fontaine et al., 2007; Balesdent et al., 2018). Fine root biomass deeper than 1 m is generally a small proportion of the total biomass in forest ecosystems (Schenk and Jackson, 2002; Pierret et al., 2016). However, the huge C stocks in deep soil layers worldwide suggest that fine root dynamics could have a strong impact, on the long-term (Rumpel and Kögel-Knabner, 2011; Stahl et al., 2016). Fine roots account for large C inputs to the soil through the release of exudates and root necromass and large amounts of C return to the atmosphere through root respiration and decomposition processes (Balesdent and Balabane, 1996; Strand et al., 2008). Estimating fine root production and turnover throughout the entire soil profile is needed to predict more accurately the potential role of forest ecosystems to mitigate climate change.

Even though fine root densities sharply decrease with soil depth, the root biomass at a depth of >1 m depth has probably been underestimated. Maeght et al. (2015) showed that >50% of the total fine root biomass was below 1 m depth in a rubber plantation in Thailand. Fine root biomass between the depths of 1.0 and 4.0 m was 5.8 t ha⁻¹ while it amounted to only 4.8 t ha⁻¹ in the 0–1 m soil layer. Soil coring and measurements of fine root intersects on deep soil trenches showed a similar pattern in Brazil for several *Eucalyptus* species with about 50% of the total fine root length at a depth of >1 m, from 1 to 6 years after planting (Laclau et al., 2013b; Pinheiro et al., 2016). In an agroforestry system in the south of France, Cardinael et al. (2015) showed that 35%

of the total fine root intersects of walnut trees on trench walls were deeper than 2 m. At the same site, using the minirhizotron technique, Germon et al. (2016) measured 25% of the total fine root production deeper than 4 m. Germon et al. (2018) showed that the proportion of fine root biomass in the 0–1 m layer relative to the total fine root biomass down to 17 m was 31% in *Eucalyptus grandis* stands, 52% in *Acacia mangium* stands and 37% in a mixture with 50% of the two species, at 4 years after planting. The proportion of deep roots increases with stand age in young stands. Fine roots below 1 m represented 10%, 30% and 42% of the total fine root biomass in 2-, 4- and 12-year-old *Ziziphus jujube* plantations in China (Ma et al., 2013). Fine root intersects on trench walls at a depth of >4 m represented 5%, 10% and 15% of total fine roots in 1-, 3.5- and 6-year-old *Eucalyptus* plantation in Brazil (Laclau et al., 2013b). The rooting depth also increased with stand age down to a maximum of 23.2 m at age 22 years in apple orchards in a sub-humid region of China, and roots deeper than 1 m accounted for 49% of the total fine root biomass at 22 years (Li et al., 2019). However, the increase of root biomass in deep soil layers can decrease water availability in sub-humid or arid climates (Fig. 5).

A recent meta-analysis of changes in stable carbon isotope

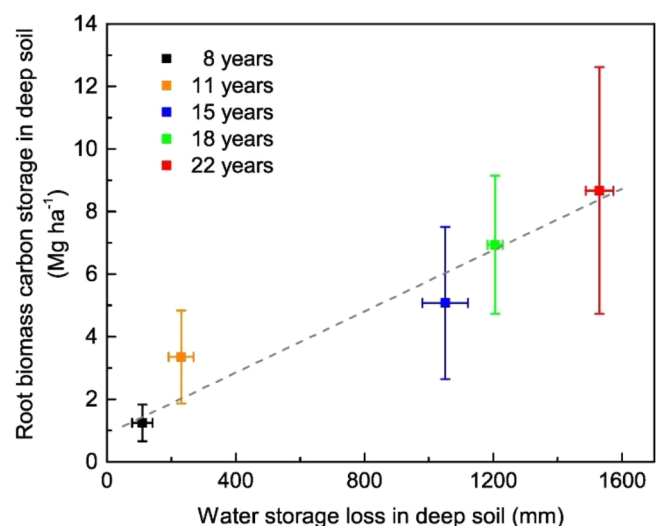


Fig. 5. Relationship between root biomass carbon storage and water storage loss relative to long-term cultivated farmlands between the depths of 1 m and 23.2 m in a chronosequence of 8-, 11-, 15-, 18-, and 22-year-old afforested apple (*Malus pumila* Mill.) orchard stands in a sub-humid region of the Chinese Loess Plateau. The standard deviations are indicated (n = 3). Adapted from Li et al. (2019), used by permission.

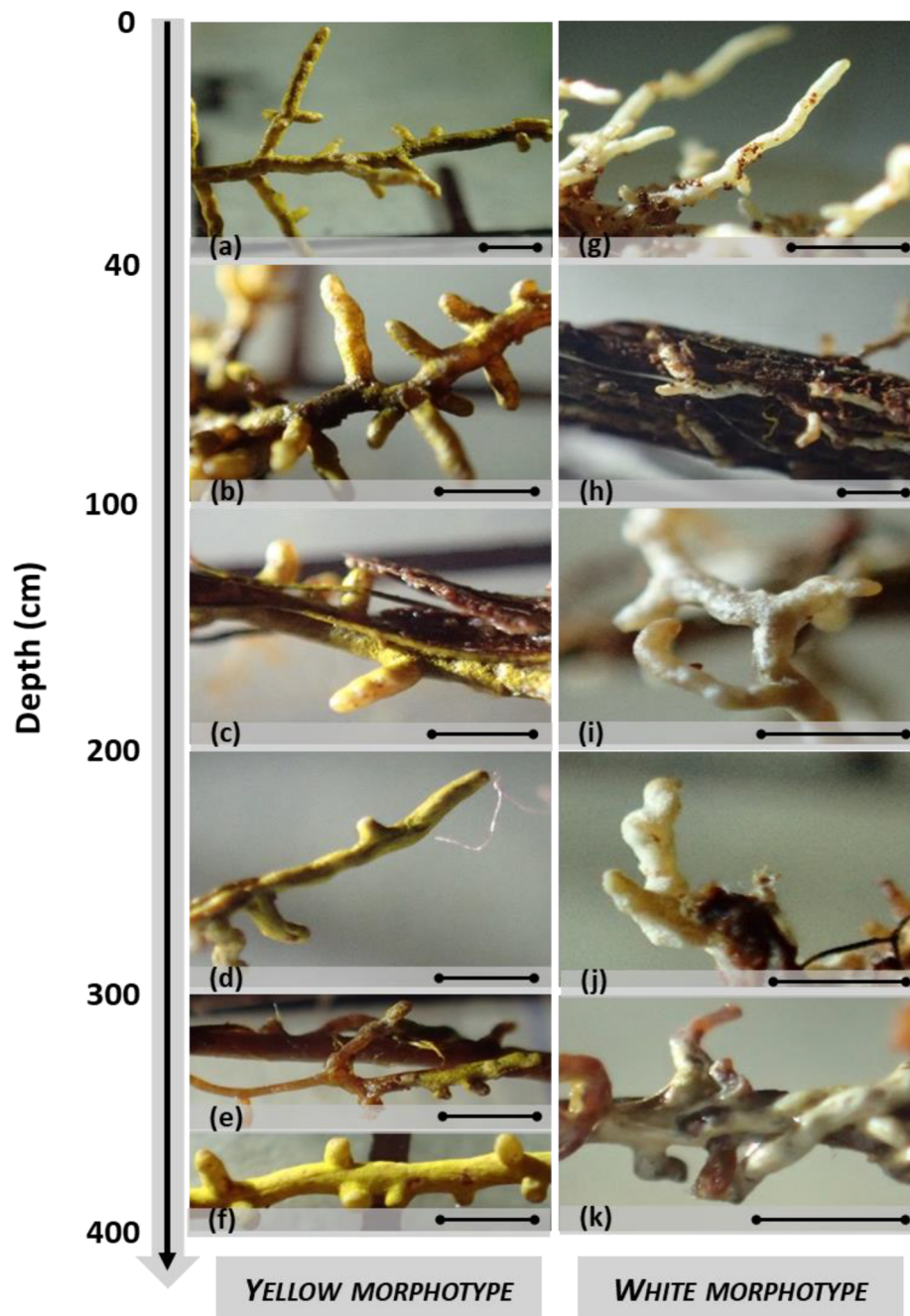


Fig. 6. Ectomycorrhizal root tips originated from 4-m deep pits in a *Eucalyptus grandis* plantation in Brazil. The yellow morphotype (a–f) was identified molecularly as *Pisolithus* spp. and the white morphotype (g–k) as *Scleroderma* spp. In each image, the scale bar corresponds to 1 mm. Adapted from Robin et al. (2019), used by permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

signatures across different climatic zones (at 112 sites) showed that the proportion of carbon allocated deeper than 30 cm was much higher than the proportion of root biomass documented in meta-analyses (Balesdent et al., 2018). This pattern could be explained by the contribution of root exudates in addition to root mortality as well as by reduced decay rates at depth. Several interacting processes could contribute to slow down decay rates at depth: scattered microbial biomass, stabilization of soil organic matter by minerals, as well as a reduced stimulation of SOC decomposition by the supply of fresh carbon (priming effect) (Fontaine et al., 2007). Fine root decomposition rates influence the ability of forest ecosystems to store C and act as a sink for CO₂. When roots are decomposed, parts of root tissues are incorporated into the soil organic matter (Strand et al., 2008). De Camargo et al.

(1999) showed that fine roots can be decomposed at least down to a depth of 5 m in eastern Amazon. Nepstad et al. (1994) estimated that C stocks deeper than 1 m exceeded SOC in the 0–1 m layer and the above-ground organic C in an Amazonian tropical forest. The deep root system of this Amazonian forest probably released large amounts of organic C into the soil through root exudation, mycorrhizal associations and fine root mortality (Nepstad et al., 1994). Moreover, the microbial biomass is much lower in deep soil layers than in the topsoil, which in combination with oxygen limitations could enhance organic C sequestration as a result of low mineralization rates (Taylor et al., 2002; Rumpel and Kögel-Knabner, 2011). Organic C derived from roots is generally more sequestered in the soil than organic C coming from the aboveground litter, which is more affected by physicochemical processes and has a

different structural composition (Rasse et al., 2005; Schmidt et al., 2011; Menichetti et al., 2015). Further studies investigating the relationships between fine root dynamics, microbial communities and soil environment throughout very deep soil profiles in contrasting pedoclimatic conditions are needed to improve the predictions of soil C storage in deep soil layers under climate change.

5. Mycorrhizal association with deep roots

Symbiotic association with root systems involving mycorrhizal fungi are common in forest ecosystems (Höberg and Höberg, 2002; Churchland and Grayston, 2014), with beneficial effects both for plants and fungi. Plants provide carbon to mycorrhizal fungi and in exchange, mycorrhizas greatly increase the volume of soil explored, which makes it possible to increase the amounts of water and nutrients taken up in the soil and transferred to the plants (Johnson and Gehring, 2007). Symbiotic associations between deep roots and mycorrhizal fungi are poorly documented and until recently, it was commonly believed that mycorrhizal associations were limited to shallow soil layers. Nevertheless, recent researches on microbial communities have highlighted the value of studying deep soil layers and showed unexpected abundant and diverse microbial communities in subsoils (Li et al., 2014; Gocke et al., 2017; Zheng et al., 2017; Pereira et al., 2018).

Most of research about arbuscular mycorrhizal (AM) fungi depending on soil depth has been carried out in agricultural systems down to a maximum depth of 1 m. The results were mainly focused on the abundance and diversity of AM spores, with few studies taking into account AM fungi root colonization (Kabir et al., 1998; Oehl et al., 2005; Cuenca and Lovera, 2010; Yang et al., 2010; Taniguchi et al., 2012; Shukla et al., 2013; Becerra et al., 2014; Gai et al., 2015). Nevertheless, some older studies report observations of mycorrhizal associations more deeply, down to a depth of 4 m (Virginia et al., 1986; Zajicek et al., 1986). In tropical agroforests with *Faidherbia albida* trees, Dalpé et al. (2000) showed that AM propagules were viable in cores taken down to a depth of 34 m, which highlights the importance of improving our knowledge of deep mycorrhizal symbioses. A recent survey showed the presence of AMF fungal spores in deep soil layers down to a depth of 8 m in pure and mixed-species plantations of *Eucalyptus grandis* and *Acacia mangium* in Brazil (Pereira et al., 2018), with root colonization rates between 6 and 25% for the 0–100 cm soil, and a decrease to about 10% below 1 m and 5%–6% below 3 m. This weak AMF colonization could be partly due to the age of the trees (over 1 year old) because the symbiosis with AM fungi is commonly known to be substituted gradually by ectomycorrhizal fungi in trees plantations (Read, 1991; Bellei et al., 1992; Boerner et al., 1996).

A vertical structuration of ectomycorrhizal (ECM) symbioses has been shown in numerous studies, with different ECM fungal communities between organic and mineral soil layers (Moyersoen et al., 1998; Dickie et al., 2002; Rosling et al., 2003; Genney et al., 2006). Unfortunately, most of the studies do not exceed the depth of 2 m (Bakker et al., 2006; Clemmensen et al., 2015; Rocha et al., 2016). ECM root tips have been observed down to a depth of 4 m in bedrock fissures (Bornyasz et al., 2005; Querejeta et al., 2007). As for AM fungi, the presence of ECM fungi propagules has been shown in very deep soil layers, down to 10 m (Santana et al., 2016). Robin et al. (2019) demonstrated for the first time using molecular sequencing that ECM symbioses occurred with *Eucalyptus grandis* roots at a depth of 4 m in Brazil (Fig. 6). The intraspecific diversity of the fungus *Pisolithus* in this study was strongly impacted by the depth, suggesting the presence of a reservoir of biodiversity associated with the deepest roots.

The occurrence of mycorrhizal associations (with both AM and ECM fungi) in deep soil layers can contribute to increasing the volume of soil explored by scarce roots, which can greatly enhance water and nutrient capture during drought periods (Lehto and Zwiazek, 2011; Begum et al., 2019). Moreover, mycorrhizal fungi have a strong impact on carbon cycling (Rillig et al., 2001; Tedersoo and Bahram, 2019), with

possible consequences on C sequestration in deep soil layers. For example, the symbiosis with ECM fungi increases the lifespan of fine roots (King et al., 2002; Guo et al., 2008; McCormack and Guo, 2014; Lambais et al., 2017), and the fungal biomass of both AM and ECM fungi can represent a significant C sink in forest ecosystems (Rillig et al., 2001; Wilson et al., 2009; Cairney, 2012; Clemmensen et al., 2015). The turnover of fungal biomass in deep soil layers can be lower than in the topsoil as a result of the low abundance of predatory organisms (Fernandez et al., 2016), which suggests that the contribution of fungi to C storage in the subsoil could be important.

There are serious technical and methodological difficulties to study mycorrhizal associations with deep roots, which explains that mycorrhizal symbioses in deep soil layers are still very little documented. The difficulty to sample a sufficient weight of mycorrhizal fungi in undisturbed soil at large depth is a major challenge. Some authors speculated that they did not sample deeply enough to determine the limits of ECM fine roots (Bakker et al., 2006). The minirhizotron method is well suited for root observations and has already been used to study the dynamics of ECM fungi (Allen and Kitajima, 2013; McCormack et al., 2017). A recent study using minirhizotrons showed typical ECM structures associated with deep roots down to 6 m in a Brazilian eucalypt plantation (Lambais et al., 2017). However, the method itself could affect mycorrhization, especially in deep soil layers (transport of spores, modification of the environment near the tube...) and might create a favorable environment for fungi growth. These interesting observations, despite their limitations, suggest the urgent need to combine several methods making it possible to study *in situ* simultaneously the dynamics of roots and mycorrhizal symbioses. We also need to go beyond diversity approaches and to study more the functional aspects of these symbioses. Although a growing body of evidence suggests that biological activity in deep soil layers is a major scientific lock poorly investigated and important to resolve to improve our understanding of the biogeochemistry of forest ecosystems, it remains a major methodological and technical challenge (Gocke et al., 2017).

6. Water and nutrient uptake in deep soil layers

The role of deep roots on water uptake by trees is well documented (Phillips et al., 2016). Deep roots are essential to sustain high tree transpiration over dry seasons, which strongly influences the Amazonian climate (Kleidon and Heimann, 2000; Saleska et al., 2007). Soil water content monitoring throughout soil profiles as well as studies using hydrogen and oxygen isotopes at specific dates make it possible to estimate at which depth water is taken up by tree roots (Guderle and Hildebrandt, 2015; Beyer et al., 2016; Koeniger et al., 2016; Trogisch et al., 2016; Beyer et al., 2018). Stahl et al. (2013) showed that 46% of the trees were extracting water at a depth of at least 1.2 m in a tropical rainforest. Trees have developed efficient strategies for the acquisition of water resources in deep soil layers, which can also help sustain shallow root functioning during drought through hydraulic redistribution (Burgess et al., 1998; Domec et al., 2004; Bleby et al., 2010). Burgess et al. (2001) have demonstrated that *Eucalyptus* species have the capacity to redistribute water from wetter deep layers into shallow soil layers through vertical and horizontal roots. Hydraulic redistribution has now been demonstrated for many tree species and modeling approaches showed that this process can strongly influence the evapotranspiration and the net carbon exchange of the ecosystem (Domec et al., 2010). Water uptake in very deep soil layers is highly dynamic in response to changes in atmospheric demand and soil water contents in the upper layers (Christina et al., 2017). A modeling approach showed that the occurrence of rainfall events, changing from a week to another, had a strong impact on which depth water uptake occurs (Fig. 7). It has also been shown that tree nutrition can greatly influence water withdrawal by roots in very deep soil layers (Christina et al., 2018). Recently, Li et al. (2019) showed that the extraction of water in deep soil

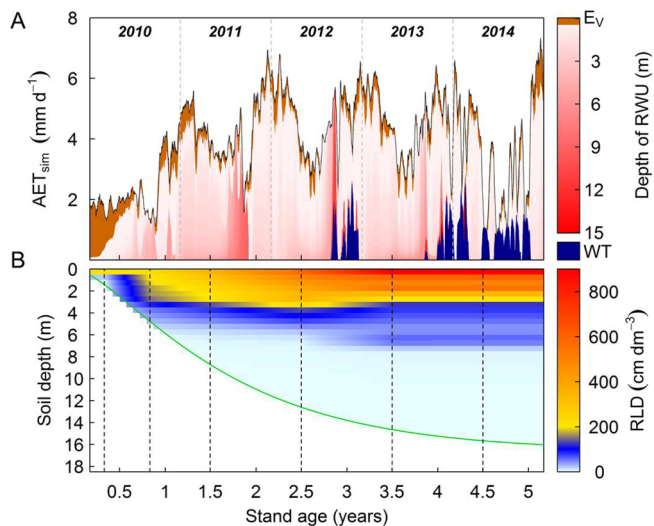


Fig. 7. Daily simulated actual evapotranspiration (AET_{sim}) using MAESPA model (A) and time series of root length density (RLD , $cm\ dm^{-3}$) (B) over 5 years after planting *Eucalyptus* trees in Brazil. The AET_{sim} (A) is represented as a function of the depth of root water uptake (RWU_{sim} , red gradient) or uptake from the capillary fringe above the water table (WT, blue), and the evaporation from the soil surface and from the wet canopy is represented in brown. Vertical lines (B) indicate the days when root profiles were measured, and the green line is the maximum measured rooting depth. Adapted from Christina et al. (2017), used by permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

layers by the root system of apple stands between 15 and 22 years of age was mainly occurring at depths below 12 m in a sub-humid region of China. They also suggested that roots in the 1–12 m layer remained alive to transport the water taken up below 12 m as they were probably unable to extract additional water in the upper 12 m. The access of roots to a very deep water table can dramatically change tree functioning and the net C exchanges in forest ecosystems (Roupsard et al., 1999; Carter and White, 2009; Zolfaghar et al., 2017). To improve soil-vegetation-atmosphere transfer models in tropical forest ecosystems, we need a better understanding of the potential of very deep roots to withdraw water stored in the subsoil (Akkermans et al., 2012).

The contribution of deep roots to supply tree requirements has been much less studied for nutrients than for water. A safety net of tree roots reducing the losses of nutrients by deep leaching is well known in agroforestry systems (Allen et al., 2004). Monitoring soil solution chemistry throughout very deep soil profiles showed that *Eucalyptus* roots take up most of the nutrients dissolved in the gravitational solutions before leaching at great depth (Laclau et al., 2010; Mareschal et al., 2013), with a very quick uptake by a root mat during the decomposition processes in the forest floor (Laclau et al., 2004). Sr and Ca cycling were also very conservative in a tropical rainforest in French Guyana, with very little Sr contribution from deep soil layers for tree species differing by their rooting depth, which supported the theory that Sr and Ca uptake and cycling are mostly superficial in tropical rainforests (Poszwa et al., 2002). Recent studies using markers suggest that a functional specialization of fine roots could also influence their ability to take up nutrients depending on the depth. Comparing oak, European beech and Norway spruce monocultures in Denmark, Göransson et al. (2006) showed that the distribution of roots and mycelia was not a reliable indicator of nutrient uptake capacity by tree roots at different soil depths. The uptake capacity from deep soil layers was higher than expected from the root distribution for most of the markers compared with the topsoil, which might be explained by an overlap of the uptake zones around the roots and mycorrhizal hyphae in the topsoil (Göransson et al., 2006). Injection of $^{15}NO_3^-$, Rb^+ (K^+ analog) and Sr^{2+} (Ca^{2+} analog) markers at the depths of 10, 50, 150

and 300 cm in Brazilian Ferralsol soils also suggested a functional specialization of fine roots with a higher capacity to take up cations in deep soil layers, in 2- and 6-year-old *Eucalyptus grandis* plantations (Da Silva et al., 2011; Bordron et al., 2019). Trees exhibit a great flexibility in their capability to adjust their root development and the uptake of soil resource in the layers where they are available (Jackson et al., 1990; Hutchings and de Kroon, 1994; Robinson, 1996). A recent study in a rainfall exclusion experiment showed that eucalypt fine root functioning can be considerably altered as a response to drought in deep soil profiles (Pradier et al., 2017). Whereas H_3O^+ and exchangeable K^+ concentrations were not influenced by the drought treatment (37% of rainfall exclusion) in the bulk soil, they were significantly higher in the rhizosphere than in the bulk soil in plots with reduced rainfall, notably at a depth of >2 m. This study suggested that root-induced weathering of K-bearing minerals contributed to increasing rhizosphere acidification and K bioavailability at great depth.

7. Influence of soil environment and resource availability

Deep roots are highly plastic in response to heterogeneous resource distributions (Hodge et al., 2009). Plants have the ability to adapt their root system to changing soil water contents, nutrient availabilities, soil physical properties, and soil atmosphere composition. The variability of environmental factors affecting root growth are buffered in deep soil layers compared to the topsoil (Voroney, 2007). Changes in fine root structure, architecture, and production with soil depth can be influenced by the spatial heterogeneity of soil resources and soil microclimate (Addo-Danso et al., 2020). Root ingrowth bags installed down to a depth of 6 m in mixed-species plantations of *Acacia mangium* and *Eucalyptus grandis* showed a remarkable capacity of very deep roots to explore resource-rich soil patches despite their low density in the soil (Germon et al., 2018). A high plasticity of fine roots has also been shown through a vertical segregation of fine roots in mixed-species forests making it possible to explore more intensively deep soil profiles than monospecific stands (Schenk et al., 1999). Some studies in agroforestry systems and forest ecosystems suggest that fine roots of the weakest competitor can be partially excluded from soil horizons where the resources limiting tree growth are concentrated (Schmid and Kazda, 2002; Mulia and Dupraz, 2006; Laclau et al., 2013a).

Plant species use a large range of rooting patterns to cope with periodic drought, from “drought tolerant strategies” with fine roots surviving in periodically dry soil to “drought avoiding strategies” shedding fine roots from dry soil horizons while rapidly developing roots in moister areas (Brunner et al., 2015; Vries et al., 2016; Bristiel et al., 2018). Soil water content is a major driver of root growth and production in deep soil layers. Adriano et al. (2017) showed that fine root mass of *Citrus sinensis* were higher in deep soil layers (between the depths of 5 m and 8 m) for rainfed trees than for irrigated trees. However, changes in SRL and SRA along soil profiles were unclear in those *Citrus* plantations, whatever the water supply regime. Schenk and Jackson (2002) showed that the maximum rooting depth in tropical ecosystems was positively correlated with the length of the dry season and negatively correlated with the annual precipitation. Wang et al. (2015) also found a highly negative correlation between root mass and soil water content down to a depth of 21 m in grasslands and shrublands in China. Drought periods commonly increase the proportion of fine roots in deep soil layers as well as specific root areas (Markesteijn and Poorter, 2009; Ma et al., 2018; Zhou et al., 2018). In a survey of 62 tropical tree species, Markesteijn and Poorter (2009) showed that trees increase the belowground biomass and the proportion of deep roots in response to dry conditions. Germon et al. (2019) showed an increase in SRL and SRA down to a depth of 16 m in response to throughfall exclusion for *Eucalyptus* trees in Brazil.

Fine root dynamics can also be influenced by the depth of the water table. Li et al. (2015) showed that the displacement of the root front of *Alhagi sparsifolia* was $0.66\ cm\ d^{-1}$ when the water table was at a depth

of 0.8 m and 1.5 cm d⁻¹ when the water table was at a depth of 2.2 m. Canham et al. (2012) showed a seasonal distribution of fine root biomass in deep soil layers in response to the fluctuations of the depth of the water table in southwest Australia. Although the physiological mechanisms remain little understood, some studies investigating the relationships between changes in water table depth and fine root dynamics suggest that an increase in water table depth could promote an increase in root elongation rates downwards (Stave et al., 2005; Canham, 2011).

The influence of soil texture on fine root distributions remains unclear. Fine root distributions were shallower in sandy soils than in clayey soils in a tropical evergreen forest (Schenk and Jackson, 2002). However, roots of *Haloxylon ammodendron* reached a depth of 10 m in a sandy soil and only 3 m in a heavy soil (Xu and Li, 2009). Comparing root distributions for *Entandrophragma cylindricum* Sprague (Meliaceae) in African semi-deciduous rainforests, Freycon et al. (2015) showed that fine root densities down to a depth of 6 m were lower in a coarse-textured Arenosol soil than in a fine-textured Ferralsol soil. The same pattern was showed by Laclau et al. (2013b) comparing fine root densities down to a depth of 10 m in sandy and clayey Ferralsol soils in the same *Eucalyptus* stand. Similarly, Robinson et al. (2006) in Australia reported that eucalypt species can reach 8–10 m deep and withdraw deep soil water (Fig. 8) despite a high bulk density (up to 2.0 g cm⁻³) in clayey subsoil. Canadell et al. (1996) cited some examples of roots reaching great depths in rocky soils, using cracks and macropores at the vicinity of rocks to grow with low mechanical constraints.

Nutrient availability can also influence fine root traits throughout deep soil profiles. Studying fine roots and nutrient distributions down to a depth of 10 m in five semi-arid and arid forests in the southwestern USA, McCulley et al. (2004) showed morphological and physiological adjustments of fine roots in response to nutrient availability. The fate of tracers injected at various depth in a Ferralsol soil suggested that NPK fertilization increased the capacity of *Eucalyptus grandis* fine roots to take up nutrients down to a depth of 3 m (Bordron et al., 2019). Moreover, NPK fertilization increased fine root density, specific root length and specific root area throughout the soil profile. However, N fertilization did not influence the fine root biomass down to a depth of 3 m in another *E. grandis* stand at the same site in Brazil (Jourdan et al., 2008). The relationships between nutrient availability throughout deep soil profiles, fine root dynamics and fine root traits are difficult to disentangle from changes in environmental conditions and further studies are needed to gain insight into the specific effect of soil nutrient contents.

Even though the consequences of elevated CO₂ concentrations in the atmosphere on plant growth has been studied in many FACE experiments, fine root responses are still little documented for trees. In a review paper, Iversen (2010) showed that high atmospheric CO₂ concentrations tend to increase root depth in forest ecosystems. However, most of the studies dealing with fine roots in FACE experiments were carried out in the upper soil layers. Fine root traits influence tree functioning (Prieto et al., 2015; Addo-Danso et al., 2020) but the scarcity of information on the influence of the rise of atmospheric CO₂ concentrations on fine roots traits at depths of >30 cm limits our understanding of the response of forests to climate change on huge areas. Studies dealing with the influence of elevated CO₂ concentrations on root distributions and fine root traits in deep soil layers are therefore urgently needed for tree species.

8. Modeling approaches to gain insight into the functioning of deep fine roots

Modeling architecture development and dynamics of the deep fine roots is hindered by the limited data available in the literature, yet necessary to parametrize and evaluate the models. Root number, root diameter, root volume, and root radial distances are the main parameters of root system biomechanics (Nicolli and Ray, 1996; Danquochin

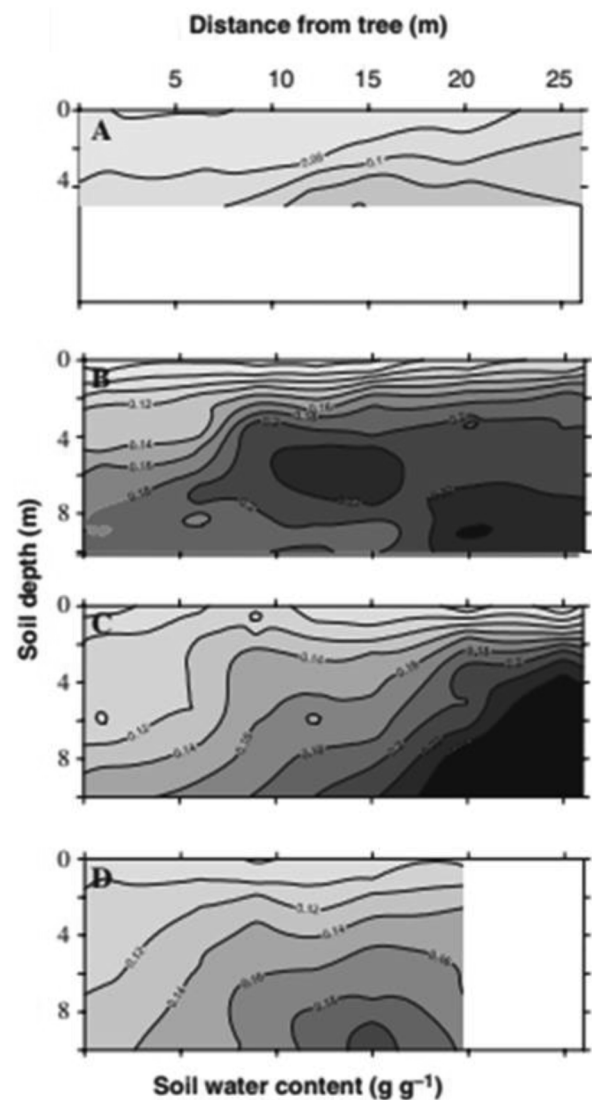


Fig. 8. Soil water content (g g⁻¹) of transects drilled to depths of up to 10 m perpendicular to eucalypt tree belts at 4 locations across south-west Western Australia (A–D). Dry areas show indirectly where eucalypt roots take up water. Adapted from Robinson et al. (2006), used by permission.

Dorval et al., 2016), varying considerably with soil layers. Soil depth strongly influences the root system architecture due to the heterogeneity of its environment. Root architectural models could simulate accurately spatial and temporal dynamics through a simulation of the root system in 3D. Integrating a vertically discretized soil into a model is particularly important as shallow and deep roots present different spatial and temporal dynamics. Model parametrization needs to consider shallow and deep-rooted systems behaving differently according to the environmental factors and soil conditions. These models can be parametrized according to the definition of root types (e.g. RootTyp from Pagès et al. (2004); or DigR (Fig. 9) from Barczy et al. (2018)) or by branching order (e.g. OpenSimRoot from Postma et al. (2017)) or through parametric L-system modeling (Leitner et al., 2010), which also might vary with soil layers. Such a model without discretized processes by soil layers is not capable to simulate accurately the impact of environmental conditions and soil resources on root development. Models devoted to simulating water and nutrient uptake dynamics need to integrate the functional specialization of deep roots and root growth plasticity in response to environmental conditions, in particular in deep soil layers. However, most root functioning rules are still not

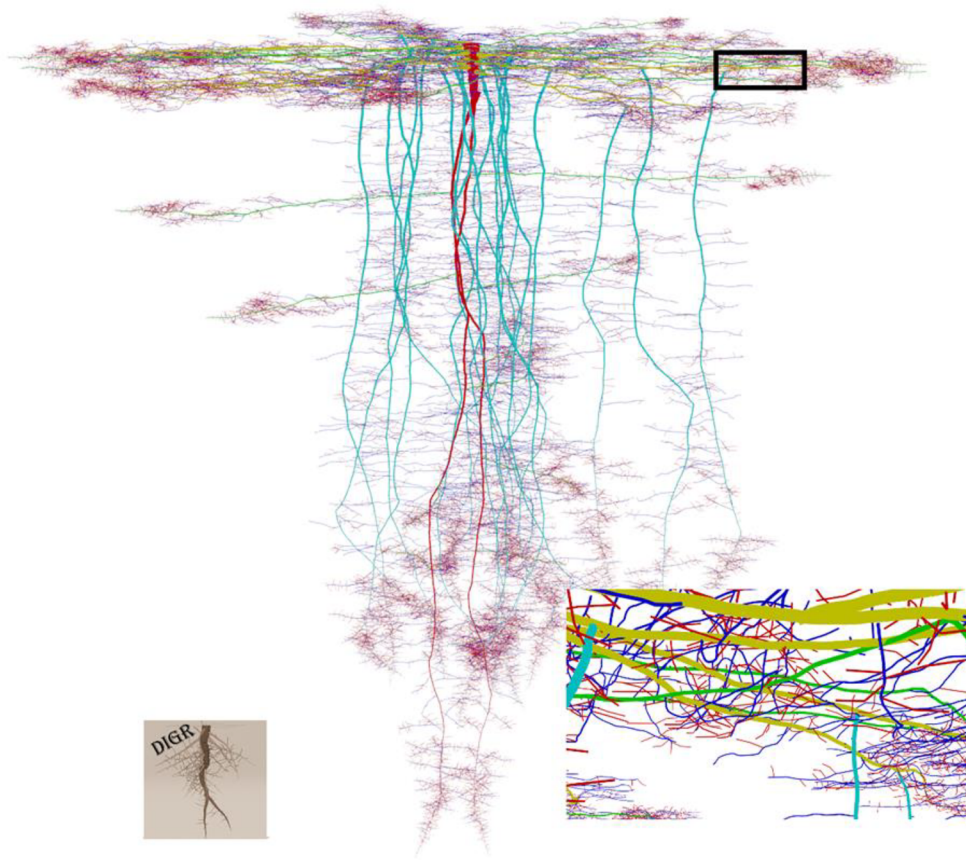


Fig. 9. Simulation of *Eucalyptus* root system by DigR model. Side view of a 5-year-old seedling (main) and detail (black rectangle) of shallow roots (bottom right). Different root types are shown: taproot (red), distal secondary taproot (light blue), plagiotropic secondary root (blue), cable-like root (yellow), long fine root (blue), medium fine root (purple), short fine root (red). DigR logo represents 2×2 m scale for the whole root system. Adapted from Barczy et al. (2018), used by permission. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

completely understood, especially at great depth as a result of the difficulty of measuring those processes *in situ*. Therefore, model calibration must cope with this knowledge and experimental limits. Architectural models can also be coupled with models simulating nutrient uptake (Mayer, 1999; Bonneau et al., 2012; Mayer et al., 2012), water transport (Doussan et al., 1998), rhizospheric processes (Kim and Silk, 1999), or even reactive transport models (Mayer, 1999; Mayer et al., 2012; Gérard et al., 2017). Nevertheless, it can be convenient to simulate accurately the overall architecture and any specialized functions of deep roots compared to shallow roots.

Furthermore, deep roots have a strong influence on deep carbon stocks, which accounts for a significant amount of carbon (Jobbágy and Jackson, 2004) and can be partially renewed at the 10-year scale (Baisden and Parfitt, 2007; Koarashi et al., 2012). Models predicting soil organic carbon stocks through a single soil layer modeling approach (Hansen et al., 1991; Sallih and Pansu, 1993; Petersen et al., 2005; Pansu et al., 2010; Oelbermann and Voroney, 2011) are therefore not considering adequately deep roots that play an active role in carbon cycling. In recent years, an awareness of the importance of deep carbon stocks by the modeling community has led to the development of different discretized models depending on the soil depth (Braakhekke et al., 2011; Braakhekke et al., 2013; Guenet et al., 2013; Taghizadeh-Toosi et al., 2014). However, modeling accurately deep root dynamics and their active role in C fluxes in forest ecosystems, as well as nutrient and water uptake throughout tree growth remains a major challenge for the next decades.

9. Conclusion

Deep roots are a major component of forest ecosystems that can

greatly influence the biogeochemistry of the Critical Zone. Their anatomical, morphological and functional root traits may be different from those of shallow roots (Fig. 2; Appendix A), with a major orientation towards the acquisition and transport of water. Climatic factors affect root phenology throughout deep soil profiles differently, as the soil environment is buffered in the deep soil layers. More research is needed to gain insight into the relationships between fine root dynamics and their anatomical, architectural and functional characteristics along deep soil profiles for a wide range of species, climates and soil properties. A high plasticity of fine roots has been shown in response to changing soil conditions from topsoil to deep soil layers (Appendix A) but the control of fine root dynamics in very deep soil layers remains little understood despite their crucial role during dry periods on huge areas of forest worldwide. Research efforts should be directed to understanding the deep-root dynamics and associated functions that could have an important influence on climate change mitigation.




Declaration of Competing Interest


























The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The financial support of the São Paulo Research Foundation scholarship (FAPESP, Projects 2015/24911-8 and 2017/13572-3) for Amandine Germon is gratefully acknowledged.

Appendix A

Main changes in fine root traits in deep soil layers compared to the topsoil.  indicates an upward trend,  indicates a downward trend and  indicates predominantly no effect. Categories of root traits and individual root traits are adapted from Brunner et al. (2015), Brunner et al. (2009), McCormack et al. (2012) and Prieto et al. (2015).

Root traits categories	Fine root traits	Trend as depth increases	Annual rainfall (Mean Temperature)	Soil type	Forest type	Topsoil		Deepest horizon		References
						Depth (cm)	Mean value	Depth (cm)	Mean value	
Growth and life span	Root length density (cm cm^{-3})		740 mm	Sandy soil	Woody evergreen species	10	6.3	130	0.2	Gwenzi et al. (2011)
	Root density (roots m^{-2})		1740 mm (24.9 °C)	Arenosol	Tropical semi deciduous forest with many evergreen taxa	0–10	3427	290–300	33	Freycon et al. (2015)
			1740 mm (24.9 °C)	Ferralsol	Tropical semi-deciduous forest	0–10	1293	290–300	353	Freycon et al. (2015)
	Fine root lifespan (days)		873 mm (15.4 °C)	Alluvial fluvisol	Silvoarable Agroforestry system with Walnut trees	0–170	167	250–470	208	Germon et al. (2016)
	Root half-life (months)		1077 mm (range from 8.3 to 40.3 °C)	Deep loamy sand	Rubber plantation	40–60	16	290–310	4	Maeght et al. (2015)
	Cumulative dead root length production (m m^{-2})		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus</i> plantation over 2 years of measurements	0–30	4.3	300–400	0.4	Lambais et al. (2017)
	Cumulative dead root length loss (cm m^{-2})		873 mm (15.4 °C)	Alluvial fluvisol	Silvoarable Agroforestry system with Walnut trees	0–70	162	400–470	19	Germon et al. (2016)
Architecture	Max root elongation rates (cm day^{-1})		1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0–100	1.16	1100–1200	4.25	Germon et al. (2019)
	Mean root elongation rate (cm day^{-1})		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus</i> plantation over 2 years of measurements	0–30	0.08	200–600	0.17–0.29	Lambais et al. (2017)
	Daily root elongation rate ($\text{cm m}^{-2} \text{ day}^{-1}$)		1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0–100	1.5	1100–1200	94.7	Germon et al. (2019)
	Root area index ($\text{m}^2 \text{ m}^{-2}$)		1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus</i> plantation	0–100	11	500–1000	2.8	Germon et al. (2019)
			1758 mm (19.5 °C)	Deep Ferralsols	Clones and seedling of <i>Eucalyptus</i>	0–100	2	500–1200	1.5	Pinheiro et al. (2016)
	Root area density ($\text{cm}^2 \text{ cm}^{-3}$)		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0–30	> 0.2	280–320	< 0.05	Bordron et al. (2019)
	Root tissue density (g cm^{-3})		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0–30	0.62	280–320	0.4	Bordron et al. (2019)
	Root length density (cm cm^{-3})		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0–30	> 2.4	280–320	< 0.5	Bordron et al. (2019)
	Root length density (mm cm^{-3})		1077 mm (range from 8.3 to 40.3 °C)	Deep loamy sand	Rubber plantation	0–10	28	4.0	0.2	Maeght et al. (2015)
	Specific root length (m g^{-1})		1390 mm (19 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	5–15	12	285–295	32	Maurice et al. (2010)
	Specific root length (m g^{-1})		1758 mm (19.5 °C)	Deep Ferralsols	Clones and seedling of <i>Eucalyptus</i>	0–100	21.3	1100–1200	36.9	Pinheiro et al. (2016)
	Specific root length (m g^{-1})		From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agroecosystems and forestry systems	0–100	12.9	100–150	12.74	Prieto et al. (2015)
	Specific root area ($\text{cm}^2 \text{ g}^{-1}$)		1758 mm (19.5 °C)	Deep Ferralsols	Clones and seedling of <i>Eucalyptus</i>	0–100	267.5	1100–1200	360.2	Pinheiro et al. (2016)
	Mean root diameter (mm)		1360 mm (20 °C)	Deep Ferrallic Arenosol	<i>Citrus sinensis</i> (L.) Osbeck plantation	0–50	0.55	700–750	0.7	Adriano et al. (2017)
	Mean root diameter (mm)		From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agroecosystems and forestry systems	0–20	0.7	100–150	0.8	Prieto et al. (2015)
	Mean root diameter (mm)		1360 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i> plantation	0–30	0.26	280–320	0.38	Bordron et al. (2019)
Anatomy	Mean conduits diameter (μm)		Ranges from 600 mm to 800 mm (from 7.9 °C in January to 27.4 °C in July)	Shallow soil on top of fractured Cretaceous limestone	<i>Juniperus ashei</i> <i>Quercus Fusiformis</i> <i>Quercus sinuata</i> <i>Brumelia lanuginosa</i>	5–10 5–10 5–10 5–10	5 42 40 30	~ 700 ~ 700 1800–2000 1800–2000	20 90 90 50	McElrone et al. (2004)
	Mean vessel diameter (μm)		1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0–50	22.8	1200–1600	51.6	Perron-Gomide et al. (Com. Pers. 2020)

	Mean vessel number	👉	1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0–50	61.9	1200–1600	10.5	Perron-Gomide et al. (Com. Pers. 2020)
	Total xylem area (cm ²)	👉	1390 mm (20 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0–50	23	1200–1600	7.8	Perron-Gomide et al. (Com. Pers. 2020)
Biotic traits	<i>Pisolithus</i> spp. diversity indice (Shannon)	👉	1360 mm (19 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0–20	1.11	350–400	1.08	Robin et al. (2019)
	<i>Pisolithus</i> spp. Richness indice (Sobs)	👉	1360 mm (19 °C)	Deep Ferralsols	<i>Eucalyptus grandis</i>	0–20	23	350–400	20	Robin et al. (2019)
Chemical traits	Carbon concentration (mg g ⁻¹)	➡	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0–20	446	100–150	445.4	Prieto et al. (2015)
	Nitrogen concentration (mg g ⁻¹)	👉	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0–20	11.3	100–150	9.7	Prieto et al. (2015)
	Soluble carbohydrate concentrations (mg g ⁻¹)	➡	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0–20	292.2	100–150	297.5	Prieto et al. (2015)
Biochemical traits	Cellulose concentration (mg g ⁻¹)	➡	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0–20	270	100–150	275.8	Prieto et al. (2015)
	Lignin concentration (mg g ⁻¹)	👉	From 950 to 3014 mm (from 1.8 to 25.7 °C)	Andosols, Entisols, Cambisols, Umbrisols, Fluvisols	agricultural, agro-ecosystems and forestry systems	0–20	216.67	100–150	221.69	Prieto et al. (2015)
Physiological traits	Sap velocity (cm h ⁻¹)	👉	630 mm (from 8° in January to 27 °C in July)	calcareous soils	deciduous <i>Bumelia la-nuginosa</i> (gum bumelia) in savannah and woodland region	0–50 cm	<0	In a cave at ~2000	>10	Bleby et al. (2010)
	Hydraulic conductivity (kg m ⁻¹ s ⁻¹ MPa ⁻¹)	👉	Ranges from 600 mm to 800 mm (from 7.9 °C in January to 27.4 °C in July)	Shallow soil on top of fractured Cretaceous limestone	<i>Bumelia lanuginosa</i> <i>Quercus fusiformis</i>	5–10 5–10	9 14	1800–2000 1800–2000	22 43	McElrone et al. (2004)
	Hydraulic conductivity (kg m ⁻² s ⁻¹ MPa ⁻¹)	👉	Ranges from 600 mm to 800 mm (from 7.9 °C in January to 27.4 °C in July)	calcareous soils	<i>Quercus fusiformis</i> Small (Texas live oak)	0–50	2e ⁻⁶	1000–2000	4e ⁻⁵	Johnson et al. (2014)
	Specific relative uptake potential of cations (Rb ⁺ and SR ²⁺ in % cm ⁻¹ cm ³)	👉	1360 mm (19 °C)	Clayey soil	<i>Eucalyptus grandis</i> plantation	0–20	>30	280–320	<20	Da Silva et al. (2011)
	Specific relative uptake potential of cations (Rb ⁺ and SR ²⁺ in % cm ⁻¹ cm ³)	👉	1360 mm (19 °C)	Sandy soil	<i>Eucalyptus grandis</i> plantation	0.20	>30	280–320	<20	Da Silva et al. (2011)
	Specific relative uptake potential of cations (Rb ⁺ and SR ²⁺ in % cm ⁻¹ cm ³)	👉	1360 mm (20 °C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	0–20	<20	280–320	>100	Bordron et al. (2019)
	Specific relative uptake of NO ₃ ⁻ (% cm ⁻¹ cm ³)	👉	1360 mm (19 °C)	Clayey soil	<i>Eucalyptus grandis</i> plantation	0–20	>60	280–320	<10	Da Silva et al. (2011)
	Specific relative uptake of NO ₃ ⁻ (% cm ⁻¹ cm ³)	👉	1360 mm (19 °C)	Sandy soil	<i>Eucalyptus grandis</i> plantation	0–20	>60	280–320	<10	Da Silva et al. (2011)
	Specific relative uptake of NO ₃ ⁻ (% cm ⁻¹ cm ³)	👉	1360 mm (20 °C)	Deep Ferrasols	<i>Eucalyptus grandis</i> plantation	0–20	20	280–320	40	Bordron et al. (2019)

References

- Addo-Danso, S.D., Defrenne, C.E., McCormack, M.L., Ostonen, I., Addo-Danso, A., Foli, E.G., Borden, K.A., Isaac, M.E., Prescott, C.E., 2020. Fine-root morphological trait variation in tropical forest ecosystems: an evidence synthesis. *Plant Ecol.* 221, 1–13.
- Adriano, E., Laclau, J.-P., Rodrigues, J.D., 2017. Deep rooting of rainfed and irrigated orange trees in Brazil. *Trees* 31, 285–297.
- Akkermans, T., Lauwaet, D., Demuzere, M., Vogel, G., Nouvellon, Y., Ardö, J., Caquet, B., De Grandcourt, A., Merbold, L., Kutsch, W., 2012. Validation and comparison of two

- soil vegetation atmosphere transfer models for tropical Africa. *J. Geophys. Res. Biogeosci.* 117.
- Allen, M.F., Kitajima, K., 2013. In situ high frequency observations of mycorrhizas. *New Phytol.* 200, 222–228.
- Allen, S.C., Jose, S., Nair, P., Brecke, B.J., Nkedi-Kizza, P., Ramsey, C.L., 2004. Safety-net role of tree roots: evidence from a pecan (*Carya illinoensis* K. Koch)–cotton (*Gossypium hirsutum* L.) alley cropping system in the southern United States. *For. Ecol. Manage.* 192, 395–407.
- Anderson, L.J., Comas, L., Lakso, A., Eissenstat, D.M., 2003. Multiple risk factors in root survivorship: A 4 year study in Concord grape. *New Phytol.* 158, 489–501.
- Annerose, D., Cornaire, B., 1994. Approche physiologique de l'adaptation à la sécheresse des espèces cultivées pour l'amélioration de la production en zones sèches. Bilan hydrique agricole et sécheresse en Afrique tropicale. John Libbey Eurotext, Paris, 137–150.
- Baddeley, J.A., Watson, C.A., 2005. Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. *Plant Soil* 276, 15–22.
- Baisden, W.T., Parfitt, R.L., 2007. Bomb ^{14}C enrichment indicates decadal C pool in deep soil? *Biogeochemistry* 85, 59–68.
- Bakker, M., Augusto, L., Achat, D., 2006. Fine root distribution of trees and understory in mature stands of maritime pine (*Pinus pinaster*) on dry and humid sites. *Plant Soil* 286, 37–51.
- Bakker, M., Jolicœur, E., Trichet, P., Augusto, L., Plassard, C., Guibert, J., Loustau, D., 2009. Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old *Pinus pinaster* stand. *Tree Physiol.* 29, 229–238.
- Balesdent, J., Balabane, M., 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biol. Biochem.* 28, 1261–1263.
- Balesdent, J., Basile-Doelsch, I., Chadoeuf, J., Cornu, S., Derrien, D., Fekiacova, Z., Hatté, C., 2018. Atmosphere–soil carbon transfer as a function of soil depth. *Nature* 559, 599–602.
- Barczy, J.-F., Rey, H., Griffon, S., Jourdan, C., 2018. DigR: a generic model and its open source simulation software to mimic three-dimensional root-system architecture diversity. *Ann. Bot.* 121, 1089–1104.
- Bastian, P., Chavarría-Krauser, A., Engwer, C., Jäger, W., Marnach, S., Ptashnyk, M., 2008. Modelling in vitro growth of dense root networks. *J. Theor. Biol.* 254, 99–109.
- Becerra, A., Bartoloni, N., Cofré, N., Soteras, F., Cabello, M., 2014. Arbuscular mycorrhizal fungi in saline soils: Vertical distribution at different soil depth. *Brazilian J. Microbiol.* 45, 585–594.
- Begum, N., Qin, C., Ahanger, M.A., Raza, S., Khan, M.I., Ahmed, N., Ashraf, M., Zhang, L., 2019. Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. *Front. Plant Sci.* 10, 1068.
- Bellei, M.D.M., Garbaye, J., Gil, M., 1992. Mycorrhizal succession in young Eucalyptus viminalis plantations in Santa Catarina (southern Brazil). *Forest Ecology and Management* 54, 205–213.
- Beyer, F., Hertel, D., Leuschner, C., 2013. Fine root morphological and functional traits in *Fagus sylvatica* and *Fraxinus excelsior* saplings as dependent on species, root order and competition. *Plant Soil* 373, 143–156.
- Beyer, M., Hamutoko, J., Wanke, H., Gaj, M., Koeniger, P., 2018. Examination of deep root water uptake using anomalies of soil water stable isotopes, depth-controlled isotopic labeling and mixing models. *J. Hydrol.* 566, 122–136.
- Beyer, M., Koeniger, P., Gaj, M., Hamutoko, J., Wanke, H., Himmelsbach, T., 2016. A deuterium-based labeling technique for the investigation of rooting depths, water uptake dynamics and unsaturated zone water transport in semiarid environments. *J. Hydrol.* 533, 627–643.
- Binkley, D., 2015. Ecosystems in four dimensions. *The New Phytologist* 206, 883.
- Bleby, T.M., McElrone, A.J., Jackson, R.B., 2010. Water uptake and hydraulic redistribution across large woody root systems to 20 m depth. *Plant, Cell Environ.* 33, 2132–2148.
- Boerner, R.E., DeMars, B.G., Leicht, P.N., 1996. Spatial patterns of mycorrhizal infectiveness of soils long a successional chronosequence. *Mycorrhiza* 6, 79–90.
- Bonneu, A., Dumont, Y., Rey, H., Jourdan, C., Fourcaud, T., 2012. A minimal continuous model for simulating growth and development of plant root systems. *Plant Soil* 354, 211–227.
- Bordron, B., Robin, A., Oliveira, I., Guillemot, J., Laclau, J.-P., Jourdan, C., Nouvellon, Y., Abreu-Junior, C., Trivelin, P., Gonçalves, J., 2019. Fertilization increases the functional specialization of fine roots in deep soil layers for young *Eucalyptus grandis* trees. *For. Ecol. Manage.* 431, 6–16.
- Bornyas, M., Graham, R., Allen, M., 2005. Ectomycorrhizae in a soil-weathered granitic bedrock regolith: linking matrix resources to plants. *Geoderma* 126, 141–160.
- Braakhekke, M.C., Beer, C., Hoosbeek, M.R., Reichstein, M., Kruijt, B., Schrumpf, M., Kabat, P., 2011. SOMPROF: A vertically explicit soil organic matter model. *Ecol. Model.* 222, 1712–1730.
- Braakhekke, M.C., Wutzler, T., Beer, C., Kattge, J., Schrumpf, M., Ahrens, B., Schöning, I., Hoosbeek, M.R., Kruijt, B., Kabat, P., 2013. Modeling the vertical soil organic matter profile using Bayesian parameter estimation. *Biogeosciences* 10, 399–420.
- Bristiel, P., Roumet, C., Violle, C., Volaire, F., 2018. Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance. *Plant Soil*. <https://doi.org/10.1007/s11104-11018-13854-11108>.
- Brunner, I., Herzog, C., Dawes, M.A., Arend, M., Sperisen, C., 2015. How tree roots respond to drought. *Front. Plant Sci.* 6, 547.
- Brunner, I., Pannatier, E.G., Frey, B., Rigling, A., Landolt, W., Zimmermann, S., Dobbertin, M., 2009. Morphological and physiological responses of Scots pine fine roots to water supply in a dry climatic region in Switzerland. *Tree Physiol.* 29, 541–550.
- Burgess, S.S., Adams, M.A., Turner, N.C., Ong, C.K., 1998. The redistribution of soil water by tree root systems. *Oecologia* 115, 306–311.
- Burgess, S.S., Adams, M.A., Turner, N.C., White, D.A., Ong, C.K., 2001. Tree roots: conduits for deep recharge of soil water. *Oecologia* 126, 158–165.
- Cairney, J.W., 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. *Soil Biol. Biochem.* 47, 198–208.
- Callesen, I., Harrison, R., Stupak, I., Hatten, J., Raulund-Rasmussen, K., Boyle, J., Clarke, N., Zabowski, D., 2016. Carbon storage and nutrient mobilization from soil minerals by deep roots and rhizospheres. *For. Ecol. Manage.* 359, 322–331.
- Canadell, J., Jackson, R., Ehleringer, J., Mooney, H., Sala, O., Schulze, E.-D., 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595.
- Canham, C., 2011. The response of Banksia roots to change in water table level in a Mediterranean-type environment. (Doctoral dissertation).
- Canham, C.A., Froend, R.H., Stock, W.D., Davies, M., 2012. Dynamics of phreatophyte root growth relative to a seasonally fluctuating water table in a Mediterranean-type environment. *Oecologia* 170, 909–916.
- Cannon, W.A., 1949. A tentative classification of root systems. *Ecology* 30, 542–548.
- Cardinael, R., Mao, Z., Prieto, I., Stokes, A., Dupraz, C., Kim, J.H., Jourdan, C., 2015. Competition with winter crops induces deeper rooting of walnut trees in a Mediterranean alley cropping agroforestry system. *Plant Soil* 391, 219–235.
- Carter, J.L., White, D.A., 2009. Plasticity in the Huber value contributes to homeostasis in leaf water relations of a mallee Eucalypt with variation to groundwater depth. *Tree Physiol.* 29, 1407–1418.
- Christina, M., Laclau, J.-P., Gonçalves, J.L.M., Jourdan, C., Nouvellon, Y., Bouillet, J.-P., 2011. Almost symmetrical vertical growth rates above and below ground in one of the world's most productive forests. *Ecosphere* 2, 1–10.
- Christina, M., Le Maire, G., Nouvellon, Y., Vezzy, R., Bordon, B., Battie-Laclau, P., Gonçalves, J.L.d.M., Delgado-Rojas, J.S., Bouillet, J.-P., Laclau, J.-P., 2018. Simulating the effects of different potassium and water supply regimes on soil water content and water table depth over a rotation of a tropical Eucalyptus grandis plantation. *Forest Ecology and Management* 418, 4–14.
- Christina, M., Nouvellon, Y., Laclau, J.-P., Stape, J.L., Bouillet, J.-P., Lambais, G.R., Maire, G., 2017. Importance of deep water uptake in tropical eucalypt forest. *Funct. Ecol.* 31, 509–519.
- Christoffersen, B.O., Restrepo-Coupe, N., Arain, M.A., Baker, I.T., Cestaro, B.P., Ciais, P., Fisher, J.B., Galbraith, D., Guan, X., Gulden, L., 2014. Mechanisms of water supply and vegetation demand govern the seasonality and magnitude of evapotranspiration in Amazonia and Cerrado. *Agric. For. Meteorol.* 191, 33–50.
- Churchland, C., Grayston, S.J., 2014. Specificity of plant-microbe interactions in the tree mycorrhizosphere biome and consequences for soil C cycling. *Front. Microbiol.* 5, 261.
- Clemmensen, K.E., Finlay, R.D., Dahlberg, A., Stenlid, J., Wardle, D.A., Lindahl, B.D., 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long term succession in boreal forests. *New Phytol.* 205, 1525–1536.
- Coll, L., Camarero, J.J., Martínez De Aragón, J., 2012. Fine root seasonal dynamics, plasticity, and mycorrhization in 2 coexisting Mediterranean oaks with contrasting aboveground phenology. *Ecoscience* 19, 238–245.
- Comas, L., Eissenstat, D., 2009. Patterns in root trait variation among 25 co-existing North American forest species. *New Phytol.* 182, 919–928.
- Cuenca, G., Lovera, M., 2010. Seasonal variation and distribution at different soil depths of arbuscular mycorrhizal fungi spores in a tropical sclerophyllous shrubland. *Botany* 88, 54–64.
- Da Silva, E.V., Bouillet, J.-P., de Moraes Gonçalves, J.L., Junior, C.H.A., Trivelin, P.C.O., Hinsinger, P., Jourdan, C., Nouvellon, Y., Stape, J.L., Laclau, J.-P., 2011. Functional specialization of Eucalyptus fine roots: contrasting potential uptake rates for nitrogen, potassium and calcium tracers at varying soil depths. *Funct. Ecol.* 25, 996–1006.
- Dalpé, Y., Diop, T., Planchette, C., Gueye, M., 2000. Glomales species associated with surface and deep rhizosphere of *Faidherbia albida* in Senegal. *Mycorrhiza* 10, 125–129.
- Danquechin Dorval, A., Meredieu, C., Danjon, F., 2016. Anchorage failure of young trees in sandy soils is prevented by a rigid central part of the root system with various designs. *Ann. Bot.* 118, 747–762.
- De Camargo, P.B., Trumbore, S.E., Martinelli, L.A., Davidson, E.A., Nepstad, D.C., Victoria, R.L., 1999. Soil carbon dynamics in regrowing forest of eastern Amazonia. *Glob. Change Biol.* 5, 693–702.
- Dickie, I.A., Xu, B., Koide, R.T., 2002. Vertical niche differentiation of ectomycorrhizal hyphae in soil as shown by T RFLP analysis. *New Phytol.* 156, 527–535.
- Diggle, A., 1988. ROOTMAP—a model in three-dimensional coordinates of the growth and structure of fibrous root systems. *Plant Soil* 105, 169–178.
- Domec, J.-C., Warren, J., Meinzer, F., Brooks, J., Coulombe, R., 2004. Native root xylem embolism and stomatal closure in stands of Douglas fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia* 141, 7–16.
- Domec, J.-C., King, J.S., Noormets, A., Treasure, E., Gavazzi, M.J., Sun, G., McNulty, S.G., 2010. Hydraulic redistribution of soil water by roots affects whole stand evapotranspiration and net ecosystem carbon exchange. *New Phytol.* 187, 171–183.
- Doussan, C., Pagès, L., Vercambre, G., 1998. Modelling of the hydraulic architecture of root systems: an integrated approach to water absorption—model description. *Ann. Bot.* 81, 213–223.
- Du, E., Fang, J., 2014. Linking belowground and aboveground phenology in two boreal forests in Northeast China. *Oecologia* 176, 883–892.
- Dunbabin, V.M., Postma, J.A., Schnepf, A., Pagès, L., Javaux, M., Wu, L., Leitner, D., Chen, Y.L., Rengel, Z., Diggle, A.J., 2013. Modelling root–soil interactions using three-dimensional models of root growth, architecture and function. *Plant Soil* 372, 93–124.
- Dupuy, L., Gregory, P.J., Bengough, A.G., 2010. Root growth models: towards a new generation of continuous approaches. *J. Exp. Bot.* 61, 2131–2143.

- Fan, P., Guo, D., 2010. Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. *Oecologia* 163, 509–515.
- Fernandez, C.W., Langley, J.A., Chapman, S., McCormack, M.L., Koide, R.T., 2016. The decomposition of ectomycorrhizal fungal necromass. *Soil Biol. Biochem.* 93, 38–49.
- Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* 450, 277.
- Freyon, V., Wonkam, C., Fayolle, A., Laclau, J.-P., Lucot, E., Jourdan, C., Cornu, G., Gourlet-Fléury, S., 2015. Tree roots can penetrate deeply in African semi-deciduous rain forests: evidence from two common soil types. *J. Trop. Ecol.* 31, 13–23.
- Friend, A.L., Coleman, M.D., Isebrands, J., 1994. Carbon allocation to root and shoot systems of woody plants. In: *Biology of Adventitious root Formation*. Springer, pp. 245–273.
- Gai, J., Gao, W., Liu, L., Chen, Q., Feng, G., Zhang, J., Christie, P., Li, X., 2015. Infectivity and community composition of arbuscular mycorrhizal fungi from different soil depths in intensively managed agricultural ecosystems. *J. Soils Sediments* 15, 1200–1211.
- Genney, D.R., Anderson, I.C., Alexander, I.J., 2006. Fine scale distribution of pine ectomycorrhizas and their extramatrical mycelium. *New Phytol.* 170, 381–390.
- Gérard, F., Blitz-Frayret, C., Hinsinger, P., Pagès, L., 2017. Modelling the interactions between root system architecture, root functions and reactive transport processes in soil. *Plant Soil* 413, 161–180.
- Germon, A., 2019. Consequences of clear-cutting on the production of fine roots, CO₂, CH₄ and N₂O down to the water table in *Eucalyptus grandis* stands conducted in coppice in a throughfall-exclusion experiment. (Doctoral dissertation).
- Germon, A., Cardinael, R., Prieto, I., Mao, Z., Kim, J., Stokes, A., Dupraz, C., Laclau, J.-P., Jourdan, C., 2016. Unexpected phenology and lifespan of shallow and deep fine roots of walnut trees grown in a silvoarable Mediterranean agroforestry system. *Plant Soil* 401, 409–426.
- Germon, A., Guerrini, I.A., Bordron, B., Bouillet, J.-P., Nouvellon, Y., de Moraes Gonçalves, J.L., Jourdan, C., Paula, R.R., Laclau, J.-P., 2018. Consequences of mixing *Acacia mangium* and *Eucalyptus grandis* trees on soil exploration by fine-roots down to a depth of 17 m. *Plant Soil* 424, 203–220.
- Germon, A., Jourdan, C., Bordron, B., Robin, A., Nouvellon, Y., Chapuis-Lardy, L., de Moraes Gonçalves, J.L., Pradier, C., Guerrini, I.A., Laclau, J.-P., 2019. Consequences of clear-cutting and drought on fine root dynamics down to 17 m in coppice-managed eucalypt plantations. *For. Ecol. Manage.* 445, 48–59.
- Gocke, M.L., Hugué, A., Derenne, S., Kolb, S., Dippold, M.A., Wiesenberger, G.L., 2017. Disentangling interactions between microbial communities and roots in deep subsoil. *Sci. Total Environ.* 575, 135–145.
- Göransson, H., Wallander, H., Ingerslev, M., Rosengren, U., 2006. Estimating the relative nutrient uptake from different soil depths in *Quercus robur*, *Fagus sylvatica* and *Picea abies*. *Plant Soil* 286, 87–97.
- Guderer, M., Hildebrandt, A., 2015. Using measured soil water contents to estimate evapotranspiration and root water uptake profiles—a comparative study. *Hydrol. Earth Syst. Sci.* 19, 409–425.
- Guenet, B., Eglin, T., Vasilyeva, N., Peylin, P., Ciais, P., Chenu, C., 2013. The relative importance of decomposition and transport mechanisms in accounting for soil organic carbon profiles. *Biogeosciences* 10, 2379–2392.
- Guo, D.L., Mitchell, R.J., Hendricks, J.J., 2004. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. *Oecologia* 140, 450–457.
- Guo, R., Li, X., Christie, P., Chen, Q., Jiang, R., Zhang, F., 2008. Influence of root zone nitrogen management and a summer catch crop on cucumber yield and soil mineral nitrogen dynamics in intensive production systems. *Plant Soil* 313, 55–70.
- Gwenzi, W., Veneklaas, E.J., Holmes, K.W., Bleby, T.M., Phillips, I.R., Hinz, C., 2011. Spatial analysis of fine root distribution on a recently constructed ecosystem in a water-limited environment. *Plant Soil* 344, 255–272.
- Hansen, S., Jensen, H., Nielsen, N., Svendsen, H., 1991. Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model DAISY. *Fertilizer Res.* 27, 245–259.
- Harrison, R.B., Footen, P.W., Strahm, B.D., 2011. Deep soil horizons: contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. *Forest Sci.* 57, 67–76.
- Hendrick, R.L., Pregitzer, K.S., 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can. J. For. Res.* 23, 2507–2520.
- Hendrick, R.L., Pregitzer, K.S., 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *J. Ecol.* 167–176.
- Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D., 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *J. Ecol.* 94, 40–57.
- Hishi, T., 2007. Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. *J. Forest Res.* 12, 126–133.
- Hodge, A., 2004. The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol.* 162, 9–24.
- Hodge, A., Berta, G., Doussan, C., Merchan, F., Crespi, M., 2009. Plant root growth, architecture and function. *Plant Soil* 321, 153–187.
- Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. *New Phytol.* 154, 791–795.
- Huck, M., Hoogenboom, G., Peterson, C.M., 1987. Soybean Root Senescence under Drought Stress 1. Minirhizotron observation tubes: methods and applications for measuring rhizosphere dynamics, 109–121.
- Hutchings, M., de Kroon, H., 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. In: *Advances in Ecological Research*. Elsevier, pp. 159–238.
- Iversen, C.M., 2010. Digging deeper: fine root responses to rising atmospheric CO₂ concentration in forested ecosystems. *New Phytol.* 186, 346–357.
- Jackson, R., Manwaring, J., Caldwell, M., 1990. Rapid physiological adjustment of roots to localized soil enrichment. *Nature* 344, 58.
- Jackson, R.B., Mooney, H., Schulze, E.-D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci.* 94, 7362–7366.
- Jackson, R.B., Schenk, H., Jobbagy, E., Canadell, J., Colello, G., Dickinson, R., Field, C., Friedlingstein, P., Heimann, M., Hibbard, K., 2000. Belowground consequences of vegetation change and their treatment in models. *Ecol. Appl.* 10, 470–483.
- Javaux, M., Schröder, T., Vanderborght, J., Vereecken, H., 2008. Use of a three-dimensional detailed modeling approach for predicting root water uptake. *Vadose Zone J.* 7, 1079–1088.
- Jo, I., Fridley, J.D., Frank, D.A., 2015. Linking above-and belowground resource use strategies for native and invasive species of temperate deciduous forests. *Biol. Invasions* 17, 1545–1554.
- Jobbágy, E.G., Jackson, R.B., 2004. Groundwater use and salinization with grassland afforestation. *Glob. Change Biol.* 10, 1299–1312.
- Johnson, D.M., Sherrard, M.E., Domec, J.-C., Jackson, R.B., 2014. Role of aquaporin activity in regulating deep and shallow root hydraulic conductance during extreme drought. *Trees* 28, 1323–1331.
- Johnson, N.C., Gehring, C.A., 2007. Mycorrhizas: symbiotic mediators of rhizosphere and ecosystem processes. In: *The Rhizosphere*. Elsevier, pp. 73–100.
- Jourdan, C., Rey, H., 1997a. Modelling and simulation of the architecture and development of the oil-palm (*Elais guineensis* Jacq.) root system. *Plant Soil* 190, 235–246.
- Jourdan, C., Rey, H., 1997b. Modelling and simulation of the architecture and development of the oil-palm (*Elais guineensis* Jacq.) root system. *Plant Soil* 190, 217–233.
- Jourdan, C., Silva, E., Gonçalves, J.L.M., Ranger, J., Moreira, R., Laclau, J.-P., 2008. Fine root production and turnover in Brazilian *Eucalyptus* plantations under contrasting nitrogen fertilization regimes. *For. Ecol. Manage.* 256, 396–404.
- Kabir, Z., O'Halloran, I., Widden, P., Hamel, C., 1998. Vertical distribution of arbuscular mycorrhizal fungi under corn (*Zea mays* L.) in no-till and conventional tillage systems. *Mycorrhiza* 8, 53–55.
- Kim, T., Silk, W., 1999. A mathematical model for pH patterns in the rhizospheres of growth zones. *Plant, Cell Environ.* 22, 1527–1538.
- King, J.S., Albaugh, T.J., Allen, H.L., Buford, M., Strain, B.R., Dougherty, P., 2002. Below ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytol.* 154, 389–398.
- Kleidon, A., Heimann, M., 2000. Assessing the role of deep rooted vegetation in the climate system with model simulations: mechanism, comparison to observations and implications for Amazonian deforestation. *Clim. Dyn.* 16, 183–199.
- Koarashi, J., Hockaday, W.C., Masiello, C.A., Trumbore, S.E., 2012. Dynamics of decadal cycling carbon in subsurface soils. *J. Geophys. Res. Biogeosci.* 117.
- Koeniger, P., Gaj, M., Beyer, M., Himmelsbach, T., 2016. Review on soil water isotope based groundwater recharge estimations. *Hydrol. Process.* 30, 2817–2834.
- Laclau, J.-P., Nouvellon, Y., Reine, C., de Moraes Gonçalves, J.L., Krusche, A.V., Jourdan, C., Le Maire, G., Bouillet, J.-P., 2013. Mixing *Eucalyptus* and *Acacia* trees leads to fine root over-yielding and vertical segregation between species. *Oecologia* 172, 903–913.
- Laclau, J.-P., Ranger, J., de Moraes Gonçalves, J.L., Maquère, V., Krusche, A.V., M'Bou, A.T., Nouvellon, Y., Saint-André, L., Bouillet, J.-P., de Cassia Piccolo, M., 2010. Biogeochemical cycles of nutrients in tropical *Eucalyptus* plantations: main features shown by intensive monitoring in Congo and Brazil. *For. Ecol. Manage.* 259, 1771–1785.
- Laclau, J.-P., Silva, E.A.D., Rodrigues Lambais, G., Bernoux, M., Le Maire, G., Stape, J.L., Bouillet, J.-P., Jourdan, C., Nouvellon, Y., 2013. Dynamics of soil exploration by fine roots down to a depth of 10 m throughout the entire rotation in *Eucalyptus grandis* plantations. *Frontiers Plant Sci.* 4, 243 doi: 210.3389/fpls.2013.00243.
- Laclau, J.P., Toutain, F., M'Bou, A.T., Arnaud, M., Joffre, R., Ranger, J., 2004. The function of the superficial root mat in the biogeochemical cycles of nutrients in Congolese *Eucalyptus* plantations. *Ann. Bot.* 93, 249–261.
- Lambais, G.R., Jourdan, C., de Cassia Piccolo, M., Germon, A., Pinheiro, R.C., Nouvellon, Y., Stape, J.L., Campoe, O.C., Robin, A., Bouillet, J.-P., 2017. Contrasting phenology of *Eucalyptus grandis* fine roots in upper and very deep soil layers in Brazil. *Plant Soil* 421, 301–318.
- Lehto, T., Zwiazek, J.J., 2011. Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21, 71–90.
- Leitner, D., Klepsch, S., Bodner, G., Schnepf, A., 2010. A dynamic root system growth model based on L-Systems. *Plant Soil* 332, 177–192.
- Li, C., Yan, K., Tang, L., Jia, Z., Li, Y., 2014. Change in deep soil microbial communities due to long-term fertilization. *Soil Biol. Biochem.* 75, 264–272.
- Li, C., Zeng, F., Zhang, B., Liu, B., Guo, Z., Gao, H., Tiyyip, T., 2015. Optimal root system strategies for desert phreatophytic seedlings in the search for groundwater. *J. Arid Land* 7, 462–474.
- Li, H., Si, B., Ma, X., Wu, P., 2019. Deep soil water extraction by apple sequesters organic carbon via root biomass rather than altering soil organic carbon content. *Sci. Total Environ.* 670, 662–671.
- López-Bucio, J., Cruz-Ramirez, A., Herrera-Estrella, L., 2003. The role of nutrient availability in regulating root architecture. *Curr. Opin. Plant Biol.* 6, 280–287.
- Lynch, J.P., Nielsen, K.L., Davis, R.D., Jablókow, A.G., 1997. SimRoot: modelling and visualization of root systems. *Plant Soil* 188, 139–151.
- Ma, L.-H., Liu, X.-L., Wang, Y.-K., 2013. Effects of drip irrigation on deep root distribution, rooting depth, and soil water profile of jujube in a semiarid region. *Plant Soil* 373, 995–1006.
- Ma, Z., Guo, D., Xu, X., Lu, M., Bardgett, R.D., Eissenstat, D.M., McCormack, M.L., Hedin, L.O., 2018. Evolutionary history resolves global organization of root functional traits. *Nature* 555, 94.
- Maeght, J.-L., Gonkhamdee, S., Clément, C., Isarangkool Na Ayutthaya, S., Stokes, A., Pierret, A., 2015. Seasonal patterns of fine root production and turnover in a mature

- rubber tree (*Hevea brasiliensis* Müll. Arg.) stand-differentiation with soil depth and implications for soil carbon stocks. *Frontiers Plant Sci.* 6, 1022.
- Maeght, J.-L., Rewald, B., Pierret, A., 2013. How to study deep roots—and why it matters. *Front. Plant Sci.* 4, 299.
- Majdi, H., Damm, E., Nylund, J.E., 2001. Longevity of mycorrhizal roots depends on branching order and nutrient availability. *New Phytol.* 150, 195–202.
- Makita, N., Hirano, Y., Mizoguchi, T., Kominami, Y., Dannoura, M., Ishii, H., Finér, L., Kanazawa, Y., 2011. Very fine roots respond to soil depth: biomass allocation, morphology, and physiology in a broad leaved temperate forest. *Ecol. Res.* 26, 95–104.
- Mareschal, L., Laclau, J.-P., Nzila, J.-D.-D., Versini, A., Koutika, L.-S., Mazoumbou, J.-C., Deleporte, P., Bouillet, J.-P., Ranger, J., 2013. Nutrient leaching and deep drainage under Eucalyptus plantations managed in short rotations after afforestation of an African savanna: two 7-year time series. *For. Ecol. Manage.* 307, 242–254.
- Markesteijn, L., Poorter, L., 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought and shade tolerance. *J. Ecol.* 97, 311–325.
- Maurice, J., Laclau, J.-P., Re, D.S., de Moraes Gonçalves, J.L., Nouvellon, Y., Bouillet, J.-P., Stape, J.L., Ranger, J., Behling, M., Chopart, J.-L., 2010. Fine root isotropy in *Eucalyptus grandis* plantations. Towards the prediction of root length densities from root counts on trench walls. *Plant Soil* 334, 261–275.
- Mayer, K., Amos, R., Molins, S., Gerard, F., 2012. Reactive transport modeling in variably saturated media with min3p: Basic model formulation and model enhancements. *Groundwater Reactive Transport Models* 186–211.
- Mayer, K.U., 1999. A numerical model for multicomponent reactive transport in variably saturated porous media. (Doctoral dissertation).
- McAdam, S.A., Brodribb, T.J., Ross, J.J., 2016. Shoot derived abscisic acid promotes root growth. *Plant, Cell Environ.* 39, 652–659.
- McCormack, M.L., Adams, T.S., Smithwick, E.A., Eissenstat, D.M., 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol.* 195, 823–831.
- McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmsaari, H.S., Hobbie, E.A., Iversen, C.M., Jackson, R.B., 2015. Redefining fine roots improves understanding of below ground contributions to terrestrial biosphere processes. *New Phytol.* 207, 505–518.
- McCormack, M.L., Fernandez, C.W., Brooks, H., Pritchard, S.G., 2017. Production dynamics of *Cenococcum geophilum* ectomycorrhizas in response to long-term elevated CO₂ and N fertilization. *Fungal Ecology* 26, 11–19.
- McCormack, M.L., Guo, D., 2014. Impacts of environmental factors on fine root lifespan. *Front. Plant Sci.* 5, 205.
- McCulley, R., Jobbagy, E., Pockman, W., Jackson, R., 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia* 141, 620–628.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178, 719–739.
- McElrone, A.J., Bichler, J., Pockman, W.T., Addington, R.N., Linder, C.R., Jackson, R.B., 2007. Aquaporin mediated changes in hydraulic conductivity of deep tree roots accessed via caves. *Plant, Cell Environ.* 30, 1411–1421.
- McElrone, A.J., Pockman, W.T., Martínez Vilalta, J., Jackson, R.B., 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytol.* 163, 507–517.
- Menichetti, L., Ekblad, A., Kätterer, T., 2015. Contribution of roots and amendments to soil carbon accumulation within the soil profile in a long-term field experiment in Sweden. *Agric. Ecosyst. Environ.* 200, 79–87.
- Moyersoen, B., Fitter, A., Alexander, I., 1998. Spatial distribution of ectomycorrhizas and arbuscular mycorrhizas in Korup National Park rain forest, Cameroon, in relation to edaphic parameters. *New Phytol.* 139, 311–320.
- Mulia, R., Dupraz, C., 2006. Unusual fine root distributions of two deciduous tree species in southern France: What consequences for modelling of tree root dynamics? *Plant Soil* 281, 71–85.
- Nardini, A., Casolo, V., Dal Borgo, A., Savi, T., Stenni, B., Bertoncin, P., Zini, L., McDowell, N.G., 2016. Rooting depth, water relations and non structural carbohydrate dynamics in three woody angiosperms differentially affected by an extreme summer drought. *Plant, Cell Environ.* 39, 618–627.
- Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E., Vieira, S., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372, 666.
- Nibau, C., Gibbs, D., Coates, J., 2008. Branching out in new directions: the control of root architecture by lateral root formation. *New Phytol.* 179, 595–614.
- Nicoll, B.C., Ray, D., 1996. Adaptive growth of tree root systems in response to wind action and site conditions. *Tree Physiol.* 16, 891–898.
- Oehl, F., Sieverding, E., Ineichen, K., Ris, E.A., Boller, T., Wiemken, A., 2005. Community structure of arbuscular mycorrhizal fungi at different soil depths in extensively and intensively managed agroecosystems. *New Phytol.* 165, 273–283.
- Oelbermann, M., Voroney, R.P., 2011. An evaluation of the century model to predict soil organic carbon: examples from Costa Rica and Canada. *Agrofor. Syst.* 82, 37–50.
- Ostonen, I., Püttsepp, Ü., Biel, C., Alberton, O., Bakker, M., Lohmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A., Pronk, A., 2007. Specific root length as an indicator of environmental change. *Plant Biosyst.* 141, 426–442.
- Ozier-Lafontaine, H., Lecompte, F., Sillon, J.F., 1999. Fractal analysis of the root architecture of *Gliricidia sepium* for the prediction of root branching, size and mass: model development and evaluation in agroforestry. *Plant Soil* 209, 167–179.
- Pagès, L., Bécel, C., Boukicim, H., Moreau, D., Nguyen, C., Voisin, A.-S., 2014. Calibration and evaluation of ArchiSimple, a simple model of root system architecture. *Ecol. Model.* 290, 76–84.
- Pagès, L., Vercambre, G., Drouet, J.-L., Lecompte, F., Collet, C., Le Bot, J., 2004. Root Typ: a generic model to depict and analyse the root system architecture. *Plant Soil* 258, 103–119.
- Pansu, M., Sarmiento, L., Rujano, M., Ablan, M., Acevedo, D., Bottner, P., 2010. Modeling organic transformations by microorganisms of soils in six contrasting ecosystems: Validation of the MOMOS model. *Global Biogeochem. Cycles* 24.
- Pate, J.S., Jeschke, W.D., Aylward, M.J., 1995. Hydraulic architecture and xylem structure of the dimorphic root systems of South-West Australian species of Proteaceae. *J. Exp. Bot.* 46, 907–915.
- Penuelas, J., Poulter, B., Sardans, J., Ciais, P., Van Der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusa, J., 2013. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* 4, 2934.
- Pereira, A.P.d.A., Santana, M.C., Bonfim, J.A., de Lourdes Mescolotti, D., Cardoso, E.J.B.N., 2018. Digging deeper to study the distribution of mycorrhizal arbuscular fungi along the soil profile in pure and mixed *Eucalyptus grandis* and *Acacia mangium* plantations. *Appl. Soil Ecol.* 128, 1–11.
- Perron-Gomide, M., Germon, A., Laclau, J.-P., Rodrigues, T.M., Jourdan, C., Com. Pers. 2020. Anatomy of deep and superficial roots of *Eucalyptus grandis* trees under rainfall reduction.
- Persson, H., 1980. Fine-root production, mortality and decomposition in forest ecosystems. *Vegetatio* 41, 101–109.
- Petersen, B.M., Berntsen, J., Hansen, S., Jensen, L.S., 2005. CN-SIM—a model for the turnover of soil organic matter. I. Long-term carbon and radiocarbon development. *Soil Biol. Biochem.* 37, 359–374.
- Phillips, R.P., Ibáñez, I., D'Orangeville, L., Hanson, P.J., Ryan, M.G., McDowell, N.G., 2016. A belowground perspective on the drought sensitivity of forests: Towards improved understanding and simulation. *For. Ecol. Manage.* 380, 309–320.
- Pierret, A., Maeght, J.-L., Clément, C., Montoro, J.-P., Hartmann, C., Gonkhamdee, S., 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. *Ann. Bot.* 118, 621–635.
- Pinheiro, R.C., Bouillet, J.-P., Bordron, B., Aló, L.L., Costa, V.E., Alvares, C.A., Van den Meersche, K., Stape, J.L., Guerrini, I.A., Laclau, J.-P., 2019. Distance from the trunk and depth of uptake of labelled nitrate for dominant and suppressed trees in Brazilian *Eucalyptus* plantations: Consequences for fertilization practices. *For. Ecol. Manage.* 447, 95–104.
- Pinheiro, R.C., de Deus Jr, J.C., Nouvellon, Y., Campoe, O.C., Stape, J.L., Aló, L.L., Guerrini, I.A., Jourdan, C., Laclau, J.-P., 2016. A fast exploration of very deep soil layers by *Eucalyptus* seedlings and clones in Brazil. *For. Ecol. Manage.* 366, 143–152.
- Postma, J.A., Kuppel, C., Owen, M.R., Mellor, N., Griffiths, M., Bennett, M.J., Lynch, J.P., Watt, M., 2017. OpenSimRoot: widening the scope and application of root architectural models. *New Phytol.* 215, 1274–1286.
- Poszwa, A., Dambrine, E., Ferry, B., Pollier, B., Loubet, M., 2002. Do deep tree roots provide nutrients to the tropical rainforest? *Biogeochemistry* 60, 97–118.
- Pradier, C., Hinsinger, P., Laclau, J.-P., Bouillet, J.-P., Guerrini, I.A., Gonçalves, J.L.M., Asensio, V., Abreu-Junior, C.H., Jourdan, C., 2017. Rainfall reduction impacts rhizosphere biogeochemistry in eucalypts grown in a deep Ferralsol in Brazil. *Plant Soil* 414, 339–354.
- Pregitzer, K.S., 2008. Tree root architecture: form and function. *The New Phytologist* 180, 562–564.
- Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L., 2002. Fine root architecture of nine North American trees. *Ecol. Monogr.* 72, 293–309.
- Pregitzer, K.S., Kube, M.E., Yu, C.K., Hendrick, R.L., 1997. Relationships among root branch order, carbon, and nitrogen in four temperate species. *Oecologia* 111, 302–308.
- Prieto, I., Roumet, C., Cardinael, R., Dupraz, C., Jourdan, C., Kim, J.H., Maeght, J.L., Mao, Z., Pierret, A., Portillo, N., 2015. Root functional parameters along a land use gradient: evidence of a community level economics spectrum. *J. Ecol.* 103, 361–373.
- Querejeta, J., Egerton-Warburton, L., Allen, M., 2007. Hydraulic lift may buffer rhizosphere hyphae against the negative effects of severe soil drying in a California Oak savanna. *Soil Biol. Biochem.* 39, 409–417.
- Radville, L., McCormack, M.L., Post, E., Eissenstat, D.M., 2016. Root phenology in a changing climate. *J. Exp. Bot.* 67, 3617–3628.
- Rasse, D.P., Rumpel, C., Dignac, M.-F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil* 269, 341–356.
- Read, D.J., 1991. Mycorrhizas in ecosystems. *Experientia* 47, 376–391.
- Reich, P.B., 2014. The world wide 'fast-slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301.
- Rewald, B., Ephrath, J.E., Rachmilevitch, S., 2011. A root is a root? Water uptake rates of Citrus root orders. *Plant, Cell Environ.* 34, 33–42.
- Rewald, B., Razaq, M., Lixue, Y., Li, J., Khan, F., Jie, Z., 2018. Root order-based traits of Manchurian walnut & larch and their plasticity under interspecific competition. *Sci. Rep.* 8, 9815.
- Richter, D.d., Billings, S.A., 2015. 'One physical system': Tansley's ecosystem as Earth's critical zone. *New Phytol.* 206, 900–912.
- Rillig, M.C., Wright, S.F., Nichols, K.A., Schmidt, W.F., Torn, M.S., 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. *Plant Soil* 233, 167–177.
- Robin, A., Pradier, C., Sanguin, H., Mahé, F., Lambais, G.R., de Araujo Pereira, A.P., Germon, A., Santana, M.C., Tisseyre, P., Pablo, A.-L., 2019. How deep can ectomycorrhizas go? A case study on *Pisolithus* down to 4 meters in a Brazilian eucalypt plantation. *Mycorrhiza* 29, 637–648.
- Robinson, D., 1996. Resource capture by localized root proliferation: why do plants bother? *Ann. Bot.* 77, 179–186.
- Robinson, N., Harper, R., Smettem, K.R.J., 2006. Soil water depletion by *Eucalyptus* spp.

- integrated into dryland agricultural systems. *Plant Soil* 286, 141–151.
- Rocha, J.H.T., de Moraes Gonçalves, J.L., Gava, J.L., de Oliveira Godinho, T., Melo, E.A., Bazani, J.H., Hubner, A., Junior, J.C.A., Wichert, M.P., 2016. Forest residue maintenance increased the wood productivity of a Eucalyptus plantation over two short rotations. *For. Ecol. Manage.* 379, 1–10.
- Rosling, A., Landeweert, R., Lindahl, B., Larsson, K.H., Kuyper, T., Taylor, A., Finlay, R., 2003. Vertical distribution of ectomycorrhizal fungal taxa in a podzol soil profile. *New Phytol.* 159, 775–783.
- Roupsard, O., Ferhi, A., Granier, A., Pallo, F., Depommier, D., Mallet, B., Joly, H., Dreyer, E., 1999. Reverse phenology and dry season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese west Africa. *Funct. Ecol.* 13, 460–472.
- Rumpel, C., Kögel-Knabner, I., 2011. Deep soil organic matter—a key but poorly understood component of terrestrial C cycle. *Plant Soil* 338, 143–158.
- Ryser, P., 2006. The mysterious root length. *Plant Soil* 286, 1–6.
- Saleska, S.R., Didan, K., Huete, A.R., Da Rocha, H.R., 2007. Amazon forests green-up during 2005 drought. *Science* 318, 612.
- Sallih, Z., Pansu, M., 1993. Modelling of soil carbon forms after organic amendment under controlled conditions. *Soil Biol. Biochem.* 25, 1755–1762.
- Santana, M.C., Pereira, A., Forti, V.A., Cardoso, E., 2016. Eucalypt as trap plant to capture associative fungi in soil samples from great depth. *Int. J. Environ. Agric. Res.* 2, 191–194.
- Schenk, H.J., Callaway, R.M., Mahall, B., 1999. Spatial root segregation: are plants territorial? In: *Advances in Ecological Research*. Elsevier, pp. 145–180.
- Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below ground/above ground allometries of plants in water limited ecosystems. *J. Ecol.* 90, 480–494.
- Schmid, I., Kazda, M., 2002. Root distribution of Norway spruce in monospecific and mixed stands on different soils. *For. Ecol. Manage.* 159, 37–47.
- Schmidt, M.W., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A., 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478, 49.
- Shibusawa, S., 1994. Modelling the branching growth fractal pattern of the maize root system. *Plant Soil* 165, 339–347.
- Shukla, A., Vyas, D., Anuradha, J., 2013. Soil depth: an overriding factor for distribution of arbuscular mycorrhizal fungi. *J. Soil Sci. Plant Nutr.* 13, 23–33.
- Sloan, V.L., Fletcher, B.J., Phoenix, G.K., 2016. Contrasting synchrony in root and leaf phenology across multiple sub Arctic plant communities. *J. Ecol.* 104, 239–248.
- Sochacki, S., Ritson, P., Brand, B., Harper, R., Dell, B., 2017. Accuracy of tree root biomass sampling methodologies for carbon mitigation projects. *Ecol. Eng.* 98, 264–274.
- Stahl, C., Freycon, V., Fontaine, S., Dezécache, C., Ponchant, L., Picon-Cochard, C., Klumpp, K., Soussana, J.-F., Blanfort, V., 2016. Soil carbon stocks after conversion of Amazonian tropical forest to grazed pasture: importance of deep soil layers. *Reg. Environ. Change* 16, 2059–2069.
- Stahl, C., Hérault, B., Rossi, V., Burban, B., Bréchet, C., Bonal, D., 2013. Depth of soil water uptake by tropical rainforest trees during dry periods: does tree dimension matter? *Oecologia* 173, 1191–1201.
- Stave, J., Oba, G., Eriksen, A.B., Nordan, I., Stenseth, N.C., 2005. Seedling growth of *Acacia tortilis* and *Faidherbia albida* in response to simulated groundwater tables. *For. Ecol. Manage.* 212, 367–375.
- Stone, E.L., Kalisz, P.J., 1991. On the maximum extent of tree roots. *For. Ecol. Manage.* 46, 59–102.
- Strand, A.E., Pritchard, S.G., McCormack, M.L., Davis, M.A., Oren, R., 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science* 319, 456–458.
- Taghizadeh-Toosi, A., Christensen, B.T., Hutchings, N.J., Vejlin, J., Kätterer, T., Glendinning, M., Olesen, J.E., 2014. C-TOOL: A simple model for simulating whole-profile carbon storage in temperate agricultural soils. *Ecol. Model.* 292, 11–25.
- Taniguchi, T., Usuki, H., Kikuchi, J., Hirobe, M., Miki, N., Fukuda, K., Zhang, G., Wang, L., Yoshikawa, K., Yamanaka, N., 2012. Colonization and community structure of root-associated microorganisms of *Sabina vulgaris* with soil depth in a semiarid desert ecosystem with shallow groundwater. *Mycorrhiza* 22, 419–428.
- Taylor, J., Wilson, B., Mills, M.S., Burns, R.G., 2002. Comparison of microbial numbers and enzymatic activities in surface soils and subsoils using various techniques. *Soil Biol. Biochem.* 34, 387–401.
- Tedersoo, L., Bahram, M., 2019. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev.* 94, 1857–1880.
- Thorup-Kristensen, K., Halberg, N., Nicolaisen, M., Olesen, J.E., Crews, T.E., Hinsinger, P., Kirkegaard, J., Pierret, A., Dresbøll, D.B., 2020. Digging deeper for agricultural resources, the value of deep rooting. *Trends Plant Sci.* 25 (4), 406–417. <https://doi.org/10.1016/j.tplants.2019.12.007>.
- Tierney, G.L., Fahey, T.J., 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Can. J. For. Res.* 32, 1692–1697.
- Trogisch, S., Salmon, Y., He, J.-S., Hector, A., Scherer-Lorenzen, M., 2016. Spatio-temporal water uptake patterns of tree saplings are not altered by interspecific interaction in the early stage of a subtropical forest. *For. Ecol. Manage.* 367, 52–61.
- Valenzuela Estrada, L.R., Vera Caraballo, V., Ruth, L.E., Eissenstat, D.M., 2008. Root anatomy, morphology, and longevity among root orders in *Vaccinium corymbosum* (Ericaceae). *Am. J. Bot.* 95, 1506–1514.
- van Noordwijk, M., Spek, L.Y., de Willigen, P., 1994. Proximal root diameter as predictor of total root size for fractal branching models. *Plant Soil* 164, 107–117.
- Virginia, R., Jenkins, M., Jarrell, W., 1986. Depth of root symbiont occurrence in soil. *Biol. Fertil. Soils* 2, 127–130.
- Vogt, K.A., Vogt, D.J., Bloomfield, J., 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. In: *Root Demographics and Their Efficiencies in Sustainable Agriculture, Grasslands and Forest Ecosystems*. Springer, pp. 687–720.
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjørnsen, H., 1995. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* 187, 159–219.
- Voroney, R.P., 2007. The soil habitat. In: *Soil Microbiology, Ecology and Biochemistry*. Elsevier, pp. 25–49.
- Vries, F.T.d., Brown, C., Stevens, C.J., 2016. Grassland species root response to drought: consequences for soil carbon and nitrogen availability. *Plant Soil* 409, 297–312.
- Wada, R., Tanikawa, T., Doi, R., Hirano, Y., 2019. Variation in the morphology of fine roots in *Cryptomeria japonica* determined by branch order-based classification. *Plant Soil* 444, 139–151.
- Wang, X., Wang, Z., Han, Y., Gu, J., Guo, D., Mei, L., 2007. Variations of fine root diameter with root order in *Manchurian ash* and *Dahurian larch* plantations. *Frontiers Forestry China* 2, 34–39.
- Wang, Y., Dong, X., Wang, H., Wang, Z., Gu, J., 2015. Root tip morphology, anatomy, chemistry and potential hydraulic conductivity vary with soil depth in three temperate hardwood species. *Tree Physiol.* 36, 99–108.
- Wang, Z., Guo, D., Wang, X., Gu, J., Mei, L., 2006. Fine root architecture, morphology, and biomass of different branch orders of two Chinese temperate tree species. *Plant Soil* 288, 155–171.
- Wells, C.E., Glenn, D.M., Eissenstat, D.M., 2002. Changes in the risk of fine root mortality with age: a case study in peach, *Prunus persica* (Rosaceae). *Am. J. Bot.* 89, 79–87.
- Wilson, G.W., Rice, C.W., Rillig, M.C., Springer, A., Hartnett, D.C., 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long term field experiments. *Ecol. Lett.* 12, 452–461.
- Wu, L., McGeachan, M., McRoberts, N., Baddeley, J., Watson, C., 2007. SPACSYS: integration of a 3D root architecture component to carbon, nitrogen and water cycling—model description. *Ecol. Model.* 200, 343–359.
- Xu, G.-Q., Li, Y., 2009. Rooting depth and leaf hydraulic conductance in the xeric tree *Haloxylon ammodendron* growing at sites of contrasting soil texture. *Funct. Plant Biol.* 35, 1234–1242.
- Yang, F., Li, G., Zhang, D., Christie, P., Li, X., Gai, J., 2010. Geographical and plant genotype effects on the formation of arbuscular mycorrhiza in *Avena sativa* and *Avena nuda* at different soil depths. *Biol. Fertil. Soils* 46, 435–443.
- Zajicek, J., Hetrick, B.D., Owensby, C., 1986. The influence of soil depth on mycorrhizal colonization of forbs in the tallgrass prairie. *Mycologia* 78, 316–320.
- Zeng, X., Dai, Y.J., Dickinson, R.E., Shaikh, M., 1998. The role of root distribution for climate simulation over land. *Geophys. Res. Lett.* 25, 4533–4536.
- Zheng, L., Zhao, X., Zhu, G., Yang, W., Xia, C., Xu, T., 2017. Occurrence and abundance of ammonia oxidizing archaea and bacteria from the surface to below the water table, in deep soil, and their contributions to nitrification. *MicrobiologyOpen* 6 e00488.
- Zhou, G., Zhou, X., Nie, Y., Bai, S.H., Zhou, L., Shao, J., Cheng, W., Wang, J., Hu, F., Fu, Y., 2018. Drought induced changes in root biomass largely result from altered root morphological traits: evidence from a synthesis of global field trials. *Plant, Cell Environ.* 41, 2589–2599.
- Zolfaghari, S., Villalobos-Vega, R., Zeppel, M., Cleverly, J., Rumman, R., Hingee, M., Boulain, N., Li, Z., Eamus, D., 2017. Transpiration of Eucalyptus woodlands across a natural gradient of depth-to-groundwater. *Tree Physiol.* 37, 961–975.